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A revision of *Weinmannia* (Cunoniaceae) in Malesia and the Pacific. 1. Introduction and an account of the species of Western Malesia, the Lesser Sunda Islands and the Moluccas

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ABSTRACT
About 40 species of the largely tropical, montane genus *Weinmannia* occur in Malesia and the Pacific belonging to two sections. Section *Fasciculata* is largely Malesian, extending eastwards to Fiji, and sect. *Leiospermum* is largely Pacific, occurring as far west as Papua New Guinea. The structure of the inflorescence provides previously unrecognised characters of taxonomic importance, especially at the sectional level. Because of the high levels of local endemism, species accounts for the whole region are divided into four parts. Descriptions, illustrations and distribution maps are provided here for four species: *W. fraxinea*, a widespread ochlospecies; *W. clemensiae*, a local endemic on ultramafic substrates in Sabah; *W. aphanoneura*, from Borneo and Sumatra, and *W. hooglandii* H.C. Hopkins & J.C. Bradford, *sp. nov.*, from Peninsular Malaysia.

KEY WORDS
Weinmannia,
Cunoniaceae,
inflorescence structure,
Malesia,
Pacific.

RÉSUMÉ
La Malésie et le Pacifique renferment environ 40 espèces de *Weinmannia* (genre essentiellement tropical et montagneux), réparties dans deux sections : sect. *Fasciculata*, présente surtout en Malésie et répandue à l'est jusqu'à Fiji ; sect. *Leiospermum*, surtout Pacifique, s'étendant à l'ouest jusqu'à la Papouasie-Nouvelle-Guinée. La structure des inflorescences fournit des caractéres d'importance taxonomique, surtout pour la distinction des sections, qui n'avaient pas été utilisés jusqu'à maintenant. En raison de l'importance de l'endémisme local, l'étude des espèces répandues dans l'ensemble de cette région est divisée en quatre parties. Des descriptions, illustrations et cartes de répartition sont fournies ici pour quatre espèces : *W. fraxinea* une ochloespèce largement répandue ; *W. clemensiae* endémique de Sabah, sur substrats ultramafiques ; *W. aphanoneura*, de Borneo et Sumatra, et *W. hooglandii* H.C. Hopkins & J.C. Bradford, *sp. nov.*, de la Péninsule malaise.

MOTS CLÉS
Weinmannia,
Cunoniaceae,
structure inflorescentielle,
Malésie,
Pacifique.

INTRODUCTION

Weinmannia is the largest and most widespread genus in the predominantly woody, southern hemisphere family, Cunoniaceae, and it contains almost half the 300 or so species of the family as it is currently circumscribed in BRUMMITT (1992). There are about 80 species in tropical America (BERNARDI 1961, 1963a), at least 30 in Madagascar and the Mascarene Islands (BERNARDI 1964, 1965; J.C. BRADFORD pers. comm.) and ca. 40 in Malesia and the Pacific (BERNARDI 1964 and this revision). The present day distribution of the genus is thus rather curious since it is absent from Africa, mainland Asia except for Peninsular Malaysia, and from Australia, which is part of the region of greatest generic diversity for the family. However, fossil leaves with affinities to *Weinmannia* (*Weinmanniaphyllum*) have been described from Oligocene deposits in Tasmania (CARPENTER & BUCHANAN 1993) suggesting that it may once have occurred in places where it is now extinct. *Weinmannia* is largely tropical and montane though it occurs in subtropical and temperate forest in South America and in New Zealand, and in lowland tropical forest in Madagascar. The taxonomic history of the genus was discussed by BERNARDI (1961).

In the most recent treatment of the Malesian-Pacific species, BERNARDI (1964) recognised 40 species in two sections but he rarely gave complete descriptions except for new taxa. In addition, much new material has become available since his work (e.g. 2/3 of the collections of *W. urdanetensis* Elmer and *W. pullei* Schltr. from the Highlands of New Guinea have been collected since 1959). R.D. HOOGLAND, who had a long-standing monographic interest in the family, started to revise *Weinmannia* for Malesia and the Pacific in the 1970s. The present study has drawn on his extensive collection of taxonomic literature, notes on morphology and typification, and a card index of specimens. However, the species concepts and descriptions are mine unless otherwise indicated.

My study was based largely on herbarium material with field observations in Malaysia, Fiji and New Caledonia. It is divided into four parts: this paper presents background information, an account of the widespread and variable *Weinmannia fraxinea* (D. Don) Miq. and of the remaining species in Western Malesia, the Lesser Sunda Islands and the Moluccas; part 2 (HOPKINS 1998a) deals with the species of Sulawesi and the Philippines; part 3 (HOPKINS 1998b) describes the species that occur in New Guinea and the islands of the western Pacific; and part 4 (HOPKINS & FLORENCE 1998) deals with the islands of the central Pacific and presents an index to taxa, including synonyms. Where appropriate, regional papers have been further divided by island group, each with a separate key. This arrangement has been adopted in part to reflect the high degree of regional and island-group endemism, in part to reflect authorship of the accounts, and in part because the problems remaining in Samoa and the Cook Islands preclude a uniform treatment of all taxa in a single alphabetical list. Those wishing to see a comprehensive key and alphabetical treatment of species for Malesia will find this eventually in *Flora Malesiana*. In the meantime, the sectional keys of BERNARDI (1964) are helpful, with some minor adjustments for new and recircumscribed taxa. An identification list of specimens seen (excluding New Zealand, Samoa and the Cook Islands) will be deposited in major herbaria or available from P.

Only one species, *Weinmannia fraxinea*, is widespread in Malesia and the western Pacific, occurring from northern Sumatra to the Solomon Islands. It is described in some detail in this paper. Where this and other species occur in more than one region (e.g. *W. urdanetensis* in the Philippines and New Guinea; *W. exigua* A.C. Sm. in the Solomon Islands and Fiji), the description and synonomy are given only once.

My species concept is morphological (see MCDADE 1995) and aims to be consistent with the definition of CRONQUIST (1978) as the smallest group that is consistently and persistently distinct and distinguishable by ordinary means. It has been suggested that over reliance on leaf characters (especially size and number of leaflets) has lead to taxonomic confusion and the over description of species in *Weinmannia*. However, there are few other characters available, as features of the flowers

and fruits are rarely taxonomically useful at the species level. Thus many taxa differ by combinations of quantitative characters, none of which is diagnostic on its own. The structure of the inflorescence has provided some new characters, particularly at the sectional level, but it is rather uniform amongst the species in Malesia.

There has been a wealth of anatomical work on Cunoniaceae and its relatives (e.g. DICKISON 1975a,b, 1977, 1980a,b, 1984; GOVIL & SAXENA 1976; HIDEUX & FERGUSON 1976; RAO & DICKISON 1985; RUTISHAUSER & DICKISON 1989) and many of the characters investigated have proved useful in understanding relationships within the family and with its close relatives (HUFFORD & DICKISON 1992). However, species delimitation in *Weinmannia* is aggravated by lack of strong morphological divergence, and anatomical characters are unlikely to be useful at this taxonomic level.

Within Cunoniaceae, *Weinmannia* is closely related to *Cunonia* (ENGLER 1930; HUFFORD & DICKISON 1992), with which it is sympatric in New Caledonia. It differs from *Cunonia* in the form of the floral disc (which is adnate to the base of the ovary in *Cunonia* and composed of either free lobes or a continuous ring, attached only at its base, in *Weinmannia*), the dehiscence of the fruit (dehiscing in a circle round the base and acropetally along the sutures, the valves remaining attached to the central column at the apex in *Cunonia*; dehiscing septicidally or septifragally from the apex, and the valves and central column remaining attached at the base in *Weinmannia*) and in the seeds (angular and often narrowly winged in *Cunonia*; ellipsoidal, comose at both ends or throughout and not winged in *Weinmannia*). HUFFORD & DICKISON's analysis also suggests a close affinity with *Pancheria* but this genus differs markedly from the other two in its capitate inflorescences.

Weinmannia has little economic importance in Malesia and the Pacific. The bark contains high levels of tannins and some species are used for tanning and firewood but few local uses are recorded. The flowers of *Weinmannia racemosa* L. f. are visited by bees which in turn produce honey on a commercial scale in New Zealand (J.C. BRADFORD pers. comm.).

ECOLOGY AND DISTRIBUTION

Weinmannia species are typically trees and shrubs of humid, montane forests, often growing where there is persistent cloud cover and quite high, well distributed rainfall. Twigs and leaf blades are often covered with mosses and other epiphytes. Within Malesia, the genus grows at mid to high elevations (up to 2600-2800 (-3000) m) in Borneo, Sulawesi and New Guinea) although a few species occur near sea level. In the Pacific, *Weinmannia* is absent from low coralline islands but widespread and sometimes abundant on the high volcanic ones. Vegetation zones here are more compressed than in Malesia, and *Weinmannia* is typically found at 300-750+ m. The genus also occurs on islands of continental origin, from 150-1550 m in New Caledonia, and from ca. 300-1180 m in New Zealand (*W. racem-osa*, fide WARDLE 1966).

Weinmannia often occurs on ridges, steep slopes and in areas of disturbance due to tree falls, landslides or volcanic eruptions. It is sometimes an early coloniser on volcanic slopes and along roadsides (e.g. *W. fraxinea* in Sabah, *Weinmannia sp.* in central Viti Levu) where it tolerates high light intensity. While it is found on a range of soil types, it often occurs on ones with atypical mineral composition, including soils derived from ultramafic substrates and on the leached soils associated with disturbed sites in cloud forest. Frequent plant associates are the ferns *Gleichenia* and *Dicranopteris* which are typical of burnt or repeatedly cut sites on impoverished soils, often rich in aluminium.

A few species have very specific ecologies (e.g. *Weinmannia clemensiae* Steenis from stunted forest on ultramafic soil) while others show considerable ecological plasticity and are found over a broad altitudinal range (e.g. *W. fraxinea* in parts of Malesia and *W. parviflora* G. Forst. in Tahiti), and both these species are morphologically very variable. *Weinmannia croftii* H.C. Hopkins from the Bismarck Archipelago is found both as an early coloniser of volcanic deposits and in adjacent closed, montane forest (D. FRODIN pers. comm.).

Most species of Malesian-Pacific *Weinmannia* have quite restricted distributions and there is a

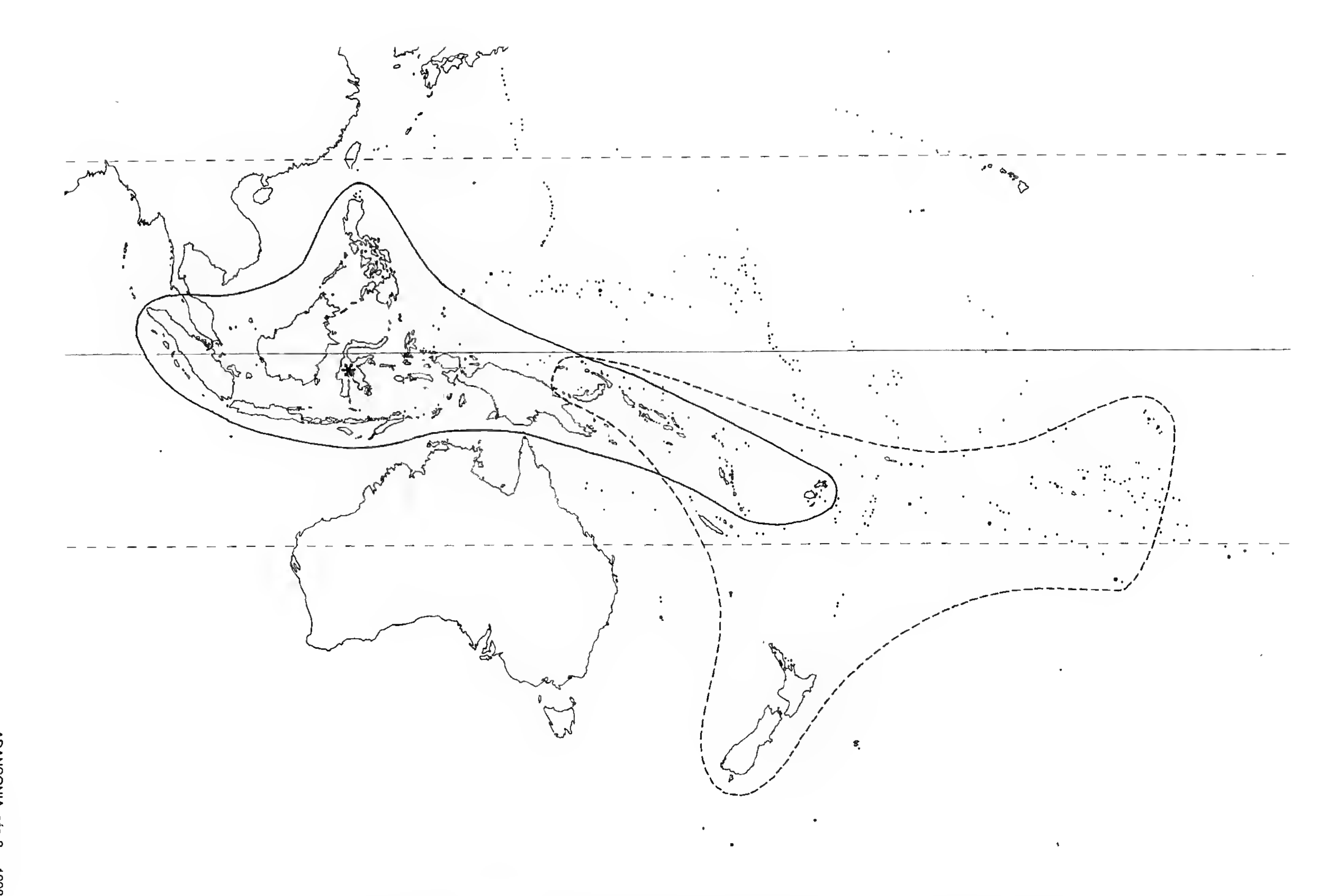


Fig. 1.—Distribution of ***Weinmannia*** sect. *Fasciculata* (solid line) and sect. *Leiospermum* (-----); ***W. descombesiana*** (✻).

high degree of island or island-group endemism. Within Malesia, *W. fraxinea* is the only widespread species. In contrast with parts of the Andes and Madagascar (J.C. BRADFORD pers. comm.), there are few sympatric or co-occurring species of *Weinmannia* in any part of its Malesian-Pacific distribution. It is of note that there are only four species in New Caledonia, which is a centre of species richness for the Cunoniaceae, with a total of about 90 species. It seems likely that here, *Weinmannia* is at least partly replaced by *Cunonia*, which is morphologically similar in many respects.

Weinmannia has small seeds that are probably wind-dispersed (see below). Anemochory, possibly with the aid of cyclones, and the opportunistic ecological strategy of some species tie in well with dispersal to, and establishment on, groups of remote volcanic islands within the Pacific. Despite the role that the break up of Gondwanaland may have played in the worldwide distribution of the genus, more recent dispersal events have clearly also had an impact.

Weinmannia is an important component of the vegetation in some parts of its distribution, such as the Society and Marquesas Islands, and New Zealand. Those species that, like *W. fraxinea*, are tolerant of natural disturbance, are likely to become more abundant with increasing human impact. However, some restricted endemics may be of conservation interest including *W. clemensiae* from the Mt. Kinabalu massif in Sabah, *W. paitensis* Schltr., which is confined to a few mountains in central and southern New Caledonia and *W. ouaiemensis* (Guillaumin & Virot) Hoogland, known from only a single locality in north-eastern New Caledonia. Some other species are known from very few collections but we have too little information at present to assess their conservation status. Several species such as *W. rapensis* F. Br. and *W. raiateensis* J.W. Moore, are endemic to small Pacific islands, but they are not currently considered threatened.

RELATIONSHIPS OF THE MALESIAN-PACIFIC SPECIES

BERNARDI (1961, 1963a,b, 1964, 1965) proposed an infrageneric classification of *Weinmannia* with six sections. According to BERNARDI, sections *Weinmannia(e)* and *Simplicifolia(e)* are principally American, with a few species in the Mascarene Islands (sect. *Weinmannia*); sections *Spicata(e)* and *Inspersa(e)* are confined to the western Indian Ocean (Madagascar and Comores); and the Malesian-Pacific species are placed in sections *Fasciculata(e)* and *Leiospermum* (referred to as sect. *Racemosae* by BERNARDI). The latter also contains two Malagasy species, *W. comorensis* Tul. and *W. baehniana* Bernardi. Sections *Fasciculata* and *Leiospermum* are distinguished from the others by the form of the floral disc, which is composed of eight free lobes alternating with the filaments, rather than a continuous ring (BERNARDI 1964: 132). In sect. *Fasciculata*, the flowers are arranged in "pseudoracemes" whilst in sect. *Leiospermum* they are dispersed, on pedicels, in racemes or panicles (BERNARDI 1964: 132).

Preliminary results of phylogenetic studies in progress, based on morphological characters, especially of the inflorescence, and on DNA sequencing (BRADFORD in press and pers. comm.) support the monophyly of both sections *Leiospermum* (morphology; DNA still unresolved) and *Fasciculata* (strong support from DNA sequences), although their relationships with other sections are still unclear. A few species were misplaced by BERNARDI; the Indian Ocean species he placed in sect. *Leiospermum* belong with the Malagasy sect. *Spicata*, and *W. descombesiana* Bernardi, placed by BERNARDI in sect. *Leiospermum*, belongs with the Malesian sect. *Fasciculata* (BRADFORD pers. comm.).

Section *Fasciculata* is a cohesive group of species. In addition to having the flowers inserted in fascicles on the inflorescence axis (to form the "pseudoracemes" of BERNARDI), these species share a common, rather complex, inflorescence plan (see below). *Weinmannia descombesiana* is somewhat problematical since it combines some characters of both sections *Fasciculata* and *Leiospermum*. Section *Fasciculata* is mostly Malesian, extending as far as east as Fiji (Fig. 1).

Section *Leiospermum* is confined to the Pacific, extending westwards as far as the Bismarck

Archipelago and Karkar Island in Papua New Guinea (Fig. 1). Most Pacific species form a closely knit group (e.g. *W. parviflora*, *W. purpurea* L.M. Perry, *W. vitiensis* Seem.). Those from New Caledonia form another group with minor differences in the flowers, which are always bisexual, and the inflorescence structure. The New Zealand species form a third group. Their flowers are inserted singly but have a greater tendancy to be perigynous and the structure of the inflorescence shows some differences from the remaining Pacific species. The species of the Marquesas Islands, at th extreme east of *Wein-mannia*'s distribution in the Pacific, have their affinities with the other Pacific species, not the American ones.

NOTES ON MORPHOLOGY AND BIOLOGY

1. Vegetative axes

Branching in most species of *Weinmannia* is from axillary buds, accompanied by the continued growth of the apical bud, and the architecture conforms to Rauh's model (Keller 1996). However, in several species of sect. *Leiospermum* the apical bud of growing shoots can be aborted and branching is then dichotomous. Most of these species show a mixture of branching patterns, but in *Weinmannia dichotoma* Brongn. & Gris, branching is almost exclusively dichotomous. Occasionally four buds at a node will develop, producing four stems of equal dominance (e.g. *W. dichotoma*, *W. affinis* A. Gray). The buds that develop in this instance are lateral to the axillary buds, and in a plane perpendicular to the line: leaf - axil - (apical bud) - axil - leaf, and are referred to as lateral, auxiliary buds; again, the apical bud is aborted.

In *Weinmannia*, as in most other Cunoniaceae, there is a pair of small, flattish, usually rounded to ovate, leaf-like structures between the petioles at each node, usually referred to as interpetiolar stipules (Rutishauser & Dickison 1989; Fig. 2A,B; 3Q). Melville (1972) described them as bud scales and considered that they were not true stipules but that each was equivalent to an entire leaf. At vegetative shoot apices, they cover the developing buds and can be either persistent or caducous as the leaves enlarge; in the later case, they leave a distinctive annular scar. Similar structures cover developing (partial) inflorescences and are also found at nodes within the inflorescence in sect. *Leiospermum* where the leaves are wholly or partly suppressed. When found in the inflorescence, the stipules are usually more oblong-elliptic than at vegetative nodes.

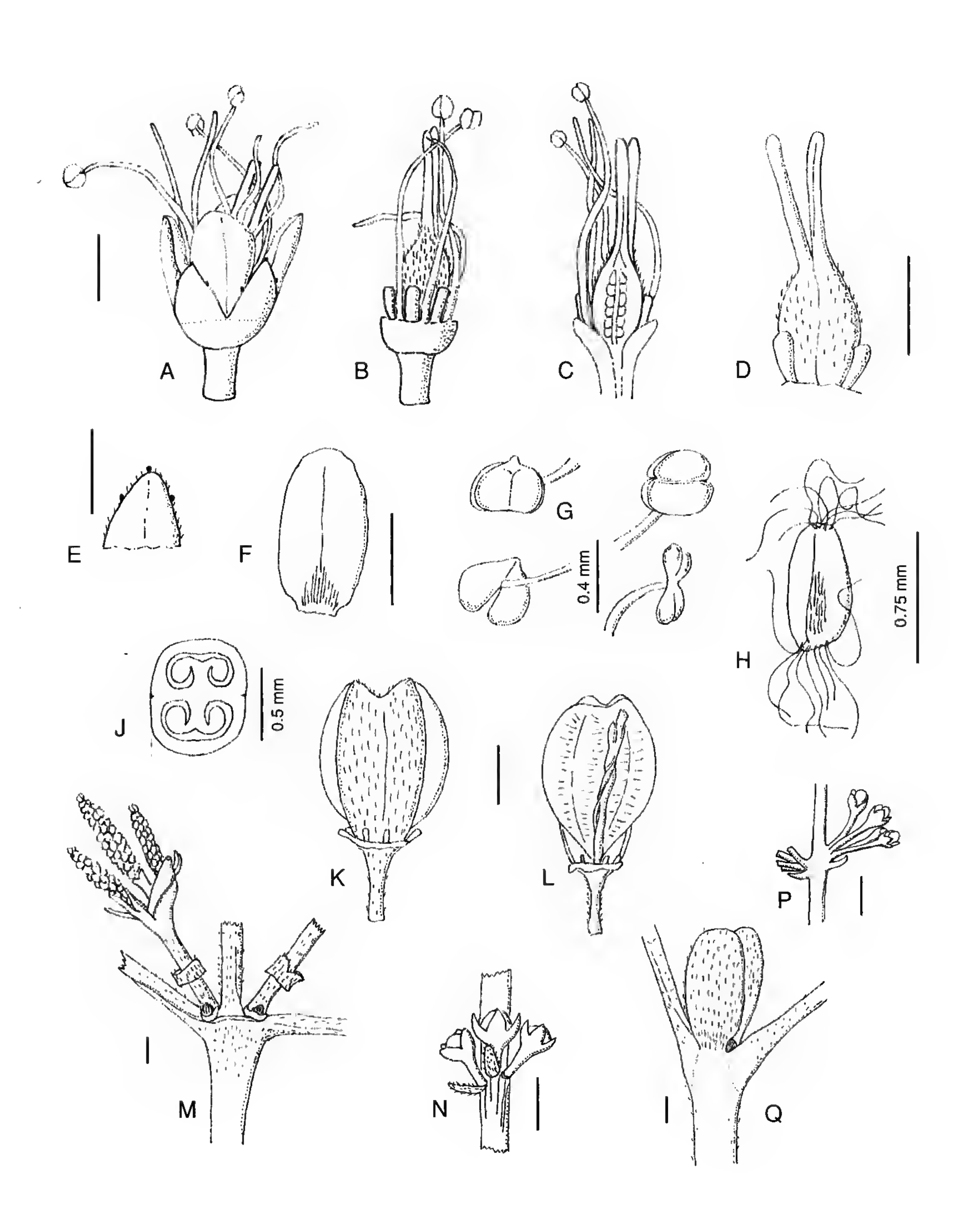
Stipules can be variable in size and shape on a single specimen and they are of varying value as taxonomic characters. They are often absent from the fertile shoots of some species and tend to be larger and more persistent on vegetative shoots.

The arrangement of leaves is always opposite and decussate, giving a distinctive appearance (Fig. 2A). Compound leaves are usually imparipinnate though the terminal leaflet is sometimes absent or fused to a lateral one. The petiole and leaf rachis can be winged or not, and sometimes the distinction between these two states is not marked. In Malesian and Pacific species, the wings are never as well developed as in some American ones. The size and shape of the leaves and leaflets, and the amount and distribution of indumentum, are often taxonomically significant. Leaflet size is small to medium, and in contrast to the Neotropics, no species is microphyllous. The margin is almost always distinctly dentate or crenate, and in *W. serrata* Brongn. & Gris, some-what sinuate. In young leaflets the ends of the teeth are pronounced and probably glandular.

The venation is rather uniform. Secondary veins usually start to branch and anastomose

Fig. 2.—A, ***Weinmannia fraxinea***, foliage of immature shoot, showing opposite and decussate compound leaves and large, rounded, salverform, interpetiolar stipules at nodes; young foliage reddish. (*Hopkins et al. 5001a*, Mt. Matang, Sarawak).—B, ***Weinmannia clemensiae***, foliage and immature fruits. Infructescence a pair of dyads with short peduncles. Note large, rounded stipules. (*Hopkins & Bradford 5010*, Pig Hill, Kinabalu, Sabah.).—C, D, ***Weinmannia fraxinea*** "*dulitensis*": C, racemes of male flowers; D, base of inflorescence showing 4 dyads subtended by a pair of opposite petioles. Note flowers inserted in fascicles. (*Hopkins & Bradford 5014*, Pig Hill, Kinabalu, Sabah).—E, ***Weinmannia richii***, fruits at dehiscence. Infructescences of dyads with very short peduncles. (*Hopkins & Bradford 5028*, road N from Monosavu Dam, Viti Levu, Fiji).—F, ***Weinmannia serrata***, immature fruits. Infructescence a central pentad and one lateral triad, with one raceme missing. (*Bradford 632*, Col d'Amieu, New Caledonia).—All photos by J.C. Bradford.


A
B
C
D
E
F


A
B
C
D
E
F
G
0.4 mm
H
0.75 mm
J
0.5 mm
K
L
P
M
N
Q

before reaching margin but at least part of the vein terminates at the tip of a tooth. Tertiary and quaternary venation are strongly reticulate. Leaf/let texture is often coriaceous or at least chartaceous-coriaceous. Species that grow at high altitudes usually have more numerous, smaller, more coriaceous leaflets than those from lower elevations. Black dots, which are probably the bases of caducous hairs, are frequent on the underside of the leaves in some species. Such leaves are referred to as "punctate" in the species descriptions. Pustules are small, pale protuberances on both the upper and lower surfaces of leaflets and they can also occur on other organs, such as the calyx lobes. They do not appear to have any taxonomic significance nor to be an artefact of drying (cf. BERNARDI 1964: 162).

Juvenile foliage and sterile collections.

The characters that are diagnostic of adult foliage are rarely evident in juvenile and coppice shoots. For instance, a series of roadside collections from sterile individuals 1-3 m high near Monasavu Dam, central Viti Levu, Fiji (*Hopkins & Bradford 5027a-h*) show a range in variation in the number, size and shape of leaflets, length of internodes, vestiture, shape of rachis, shape and persistence of stipules. Both *W. richii* and *W. affinis* occur in this area but the sterile collections were rarely consistent with the adult foliage of either of them. Some of this variation could perhaps be due to hybridization and the colonization of disturbed roadsides by hybrid swarms. Characters of mature foliage are best seen in leaves at the periphery of the crown in mature individuals (i.e. foliage from just below the inflorescences).

Fig. 3.—Details of the nodes, buds, flowers and fruits of ***Weinmannia***: **A**, flower; **B**, flower with calyx and corolla removed to reveal disc lobes, filaments and gynoecium; **C**, l.s. through B to show ovules; **D**, gynoecium with syncarpous ovary and 2 disc lobes; note groove down style and down side of ovary; **E**, calyx lobe with ciliolate margin and 3 glands; **F**, petal; **G**, anthers, L.H.S. before dehiscence, R.H.S. after dehiscence; **H**, seed with hair tuft at each end and sculptured surface; note raphe down midline; **J**, t.s. ovary (D) to show developing ovules; **K**, outer surface of one valve of a capsule showing exocarp (central part strigose) and endocarp extended as wings at both sides, on receptacle, the calyx lobes fallen but disc lobes persistent; **L**, inner surface of K, note persistent central column and minutely sculptured shiny endocarp; **M**, developing inflorescence, one lateral triad shown in axil of petiole, note stipular scar between petioles, "collars" around lateral peduncles and conical ciliate buds at base of lateral peduncles (lateral auxiliary buds); at base of triad there is a stipule (partly folded back) and a pair of much reduced leaves; **N**, section of axis of a raceme typical of sect. *Leiospermum*, the pedicels inserted singly in the axils of the bracts; **P**, section of axis of a raceme in sect. *Fasciculata*, the pedicels inserted in fascicles in the axils of the bracts; **Q**, stipules between leaf petioles at most distal node of shoot protecting apical bud. Scale bars 1 mm unless otherwise indicated. [A-F, J, *W. paitensis* (*McPherson 3403*); G, *W. serrata* (*Bernardi 12816*); H, *W. serrata* (*Balansa 204*); K, L, *W. paitensis* (*Veillon 296*); M, *W. serrata* (*Brinon 746*); N, *W. serrata* (*Balansa 2859*); P, *W. fraxinea "dulitensis"* (*Hopkins & Bradford 5014*); Q, *W. serrata* (*Lécard s.n.*, reçu 20 Oct. 1879)].—Drawn by H.C.F. HOPKINS.

2. Structure of the inflorescence (with J.C. BRADFORD)

The parts of the inflorescence are organised hierarchically, and in *Weinmannia*, there are typically three levels of organisation: 1) flowers, borne along an unbranched axis, here termed a raceme; 2) racemes, organised into metameric units, each referred to here as a partial inflorescence (PI); 3) partial inflorescences, borne along the main stem. Together, the structure of a raceme, the way the racemes are organised into a PI, and the arrangement of the PIs along the main stem, constitute the inflorescence. Although there is some interaction amongst levels of organisation, with higher levels influencing lower ones, most variation within one level of organisation appears to be independent of variation at another level. For this reason, each level of organisation will be discussed separately.

There are several terms that require short definitions so that the descriptions of the inflorescences and their component parts can be made clearly and concisely. A bract is a minute, often carinate blade along the axis of a raceme and it subtends a flower or a group of flowers. A bud is an undeveloped shoot or flower, which in *Weinmannia* is normally enclosed by a bract (flowers) or a pair of stipules (shoots). A stipule is a small leaf-like structure at a node, decussate with the true leaves that may themselves be partially or wholly suppressed at nodes within the inflorescence. A metamer is a unit which consists of an internode, the node at its distal end, and the organs and meristems (buds) associated with that node. The term "main stem" is used for any dominant, linear axis of growth.

a) ***Racemes.***—The flowers of the Malesian-Pacific species are pedicellate and borne in racemes ca. 5-12 cm long. The bracts usually fall when the flowers are still at the bud stage but occasionally they persist until fruiting. After they have fallen, a minute scar is usually visible. The individual flowers or fascicles are rather irregularly arranged on the axis of each raceme and insertion is never truly verticillate though it may superficially appear to be. Racemes may bear flowers for the whole of their length or usually they are devoid of flowers towards the base. The flowers in one raceme open more or less simultaneously.

— Sect. *Fasciculata.* Several pedicels are inserted in a small cluster in the axil of a bract (Fig. 3P). Occasionally flowers are inserted in fascicles for the most part but with some inserted singly towards the apex of the raceme, and in a few species, the fascicles tend to dissociate from the bracts during development. BERNARDI (1964: 132) used the term "pseudoraceme" in reference to sect. *Fasciculata,* but since this term is rather ambiguous, it is not used here.

— Sect. *Leiospermum.* The pedicels of the flowers are inserted singly in the axil of a bract (Fig. 3N).

b) ***Partial inflorescences.***—In general, a PI is any subunit(s) into which the inflorescence can be divided. As used here, it consists of racemes and one or more sterile stem sections which form a developmentally integrated unit whose structure is predictable within different taxonomic groups. However, sometimes (though rarely in this region) the inflorescence of *Weinmannia* is composed of individual racemes inserted in leaf axils, in which case the racemes could be considered to be the PIs.

— Sect. *Fasciculata.* A partial inflorescence is limited to a single metamer. An even number of racemes (2 or 4) are inserted at the distal node of a short, sterile stem segment (referred to as a peduncle in the species descriptions) to form either a *dyad* (Fig. 4A) or a *tetrad* (Fig. 4B). Leaf production is usually totally suppressed at the node from which the racemes arise (exceptions seen in *W. pullei*).

There is typically a small bud in the angle between the central pair of racemes at the apex of the peduncle. This bud has the potential to continue vegetative growth after flowering. Usually it is dormant during flowering (proleptic) or rarely sylleptic (i.e. no cessation of growth).

— Sect. *Leiopsermum.* A partial inflorescence can consist of more than one metamer. Usually, an odd number of racemes are inserted at one or more nodes along the axis of the PI as the terminal meristem develops into a raceme. Therefore, when the PI consists of one metamer, there are 3 racemes (called a *triad,* Fig. 4F), when of two metamers, there are 5 racemes (a *pentad,* Fig. 4G), and when of three metamers, there are 7 racemes (a *heptad*). In a few species the PIs are dyads (Fig. 4H) and the bud between the bases of the racemes has aborted (i.e. failed to develop into a third raceme; exceptions in New Zealand are described below). The basal internode of a PI may be loosely termed the peduncle.

Leaf production can be either partially or totally suppressed within each PI and when leaves are produced, they are much reduced (e.g. Fig. 4J, level Y). There are often stipules at nodes within a PI. Quite often there are "collars" around the base of the peduncles of lateral PIs (Fig. 3M). These appear to be the remnants of a pair of stipules which once covered the developing PI and were fused to each other at the base. They are not usually seen around the peduncle of the central PI in sect. *Leiospermum,* nor around the peduncles in sect. *Fasciculata.*

c) ***Inflorescences.***—An inflorescence is composed of one or more partial inflorescences. Usually all the flowers in one inflorescence open more or less simultaneously.

— Sect. *Fasciculata* (Fig. 4A-E). The PIs develop in opposite pairs from lateral meristems at a node on the main stem, i.e. they are usually in the axils of leaves. Each PI is a dyad or a tetrad. The most distal vegetative node on a stem usually produces more pairs of PIs than do subdistal nodes (see discussion of supernumerary buds below) and often the initiation of PIs is confined to the most distal node on the main stem.

Since the PIs are lateral, the apical meristem of the main stem remains indeterminate. It is normally dormant during flowering and continues vegetative growth after fruiting (prolepsis) or rarely it may be sylleptic. In exceptional cases, the apical meristem gives rise to a medial PI but

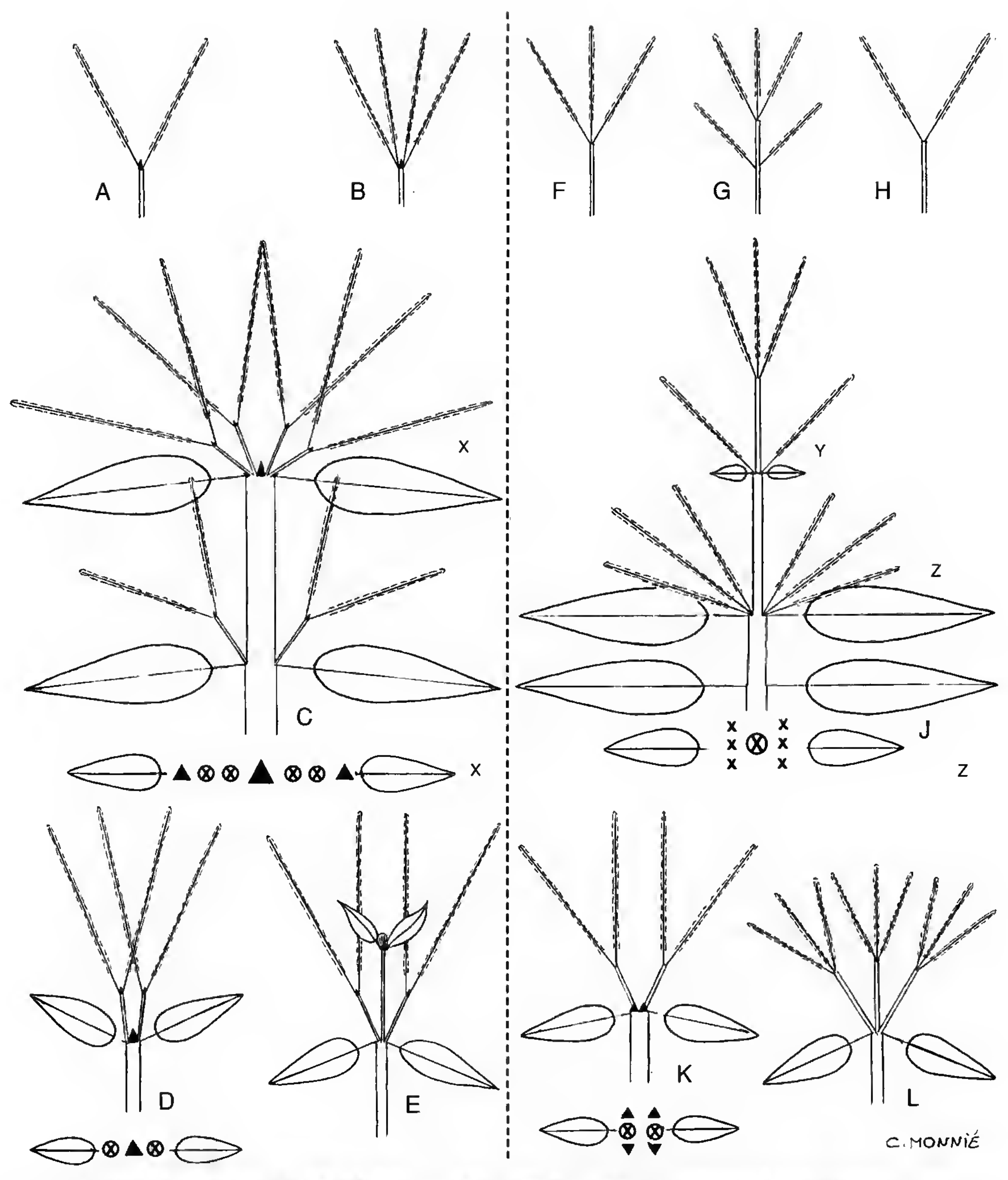


Fig. 4.—Inflorescence structure in ***Weinmannia*. A-E**, sect. ***Fasciculata***: A, B: partial inflorescences: **A**, dyad; **B**, tetrad; **C**, inflorescence typical of *W. fraxinea* group, composed of 4 dyads and a pair of lateral supernumerary buds at the most distal vegetative node and single dyads in the axils of a pair of more proximal leaves; apical bud proleptic; **D**, inflorescence typical of *W. urdanetensis* group, composed of a pair of axillary dyads; apical bud proleptic; **E**, as D, but apical bud sylleptic. **F-L**, sect. ***Leiospermum***: F-H: partial inflorescences: **F**, triad; **G**, pentad; **H**, dyad with central raceme aborted; **J**, inflorescence typical of *W. parviflora*, consisting of a heptad with 2 additional pairs of racemes inserted at node Z; partially suppressed leaves at node Y; **K**, inflorescence typical of *W. dichotoma*, with 2 axillary partial inflorescences (both dyads here) and apical bud aborted. Note prominent auxiliary buds in lateral positions at base of peduncles; **L**, inflorescence of 3 partial inflorescences (all triads). ▲: bud; ⊗: peduncle; ×: raceme.—Drawn by C. MONNIÉ.

vegetative growth can again continue from the indeterminate apical meristem within that PI.

In most species (e.g. *W. fraxinea*, *W. hutchinsonii* Merr.) there is typically more than one bud per axil with the potential to produce a PI and these "supernumerary buds" are inserted in series. One, two or three buds may develop per axil, producing one to three pairs of PIs. Level X of Fig. 4C shows 2 pairs of dyads and one pair of dormant supernumerary buds. The racemes are arranged in a plane that is perpendicular to that formed by the line: leaf - (bud) - peduncle - peduncle - apical bud - peduncle - peduncle - (bud) - leaf (see Fig. 2D).

In another group of species (e.g. *W. urdanetensis*, *W. pullei*) there are typically only two PIs (here dyads) which are inserted in the opposite axils of the most distal pair of leaves (Fig. 4D). Sometimes there are additional PIs in the axils of more proximal leaves as well but there are no additional buds in series at the same nodes as the dyads (i.e. there is only one bud per leaf axil with the potential to produce a PI). The apical bud of the main stem can be either proleptic or sylleptic (Fig. 4E), in which case the dyads that were initially at the most distal node become subdistal.

— Sect. *Leiospermum* (Fig. 4F-L, 5). Partial inflorescences are usually positioned medially and often laterally too. In some cases, the apical bud of the main stem aborts and only lateral PIs are produced. The switch to flowering usually terminates the vegetative growth of the main stem. In any one inflorescence there is usually an odd number of PIs (usually 1 or 3; rarely 2, a character state seen most frequently in some species in New Caledonia); when there is more than one, they are not always identical and the medial PI often contains more metamers than the lateral ones.

In the simplest examples (e.g. *Weinmannia marquesana* F. Br.) the inflorescence consists of a single PI (a triad or pentad) which develops from the apical bud of the main stem; the lower pair of racemes may be in the axils of either fully developed, partially suppressed or totally suppressed leaves. When an inflorescence consists of more than one PI, there are usually 3 triads (Fig. 4L) or a central pentad with a pair of axillary triads (as often seen in *W. serrata* and *W. affinis*), and occasionally more complex arrangements are found.

A unique structure is seen in *Weinmannia parviflora* (Fig. 4J). The inflorescence illustrated consists of a central heptad with a pair of partially suppressed leaves at one node, and 2 additional pairs of racemes at the lowest reproductive node. These additional racemes arise in a plane perpendicular to that formed by the line: leaf - raceme - central axis - raceme - leaf (see Fig. 4J, level Z), i.e. they are lateral to the axillary raceme and not inserted in series. One possible explanation for their presence is that the three racemes arising on either side of this node represent a pair of reduced triads in which the peduncle has not developed. Evidence for this is the occasional growth of a tiny section of peduncle in this axil

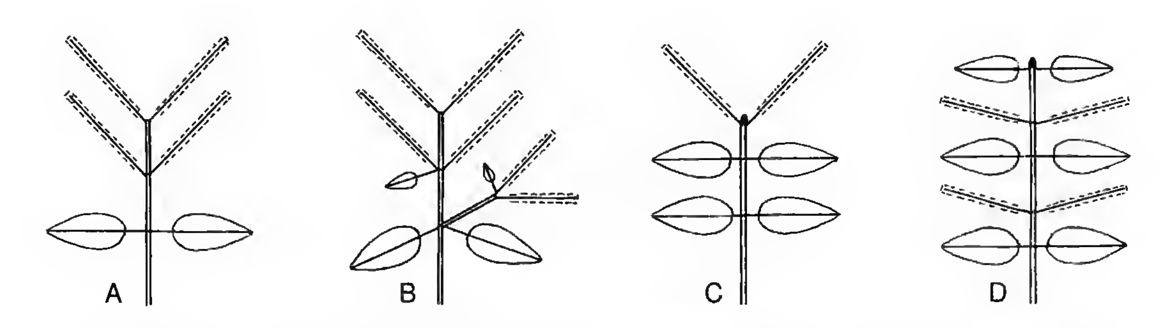


Fig. 5.—Inflorescence structure in the New Zealand species of ***Weinmannia***. **A**, **B**, ***W. sylvicola***: **A**, 2 sequential pairs of dyads (pentad minus central raceme?); apical bud aborted; **B**, as A with an additional partial inflorescence (dyad) in an axillary position at subdistal node; **C**, **D**, ***W. racemosa***: **C**, inflorescence a median dyad, apical bud proleptic; **D**, as C but apical bud sylleptic, and continuing to produce dyads and leaves at sequential nodes.—Drawn by H.C.F. Hopkins.

(see illustration of *W. rarotongensis* Hemsl., Fig. 7G in HOPKINS & FLORENCE 1998).

In three of the New Caledonian species and occasionally in other Pacific ones, the apical bud of the main stem may abort. In *Weinmannia dichotoma* for instance, the inflorescence frequently consists of two lateral PIs that develop at the most distal leaf-bearing node (Fig. 4K). These PIs can be either triads (Fig. 4F) or dyads (Fig. 4H,K), where the apical meristem within the PI has aborted also. At the node from which the PIs arise, there are often prominent lateral buds in a plane perpendicular to that of the leaves (lateral, auxiliary buds, Fig. 4K). They are most obvious in *W. dichotoma* but occur in other species as well.

In both species from New Zealand, *Weinmannia sylvicola* Sol. ex A. Cunn. and *W. racemosa*, the inflorescence structure is unique although it can still be understood as part of the pattern found in sect. *Leiospermum* (Fig. 5).

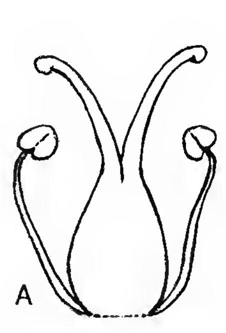
In *Weinmannia sylvicola*, the inflorescence is similar to those already described for sect. *Leiospermum* in which PIs consist of more than one metamer and they can develop in both medial and lateral positions. However, *W. sylvicola* is distinctive in that the apical meristem usually aborts (rarely not, e.g. *Colenso s.n.* where it appears dormant), so that the PI in a medial position resembles a pentad without the central raceme (Fig. 5A). In this instance, the apical meristem of both the PI and the main stem is the same. Apical meristems commonly abort in three of the species from New Caledonia but then the PI consists of only a single metamer, though in some other Pacific species where the apical meristem of the main stem sometimes aborts, lateral PIs may be pentads or heptads (e.g. *W. purpurea* L.M. Perry) and consist of more than one metamer. As in other pentad inflorescences, leaf production in *W. sylvicola* may be normal, partially or totally suppressed at the node from which the lower pair of racemes arise. When lateral PIs develop, they usually consist of only one metamer and often they develop at only one side to produce an asymmetrical inflorescence (Fig. 5B).

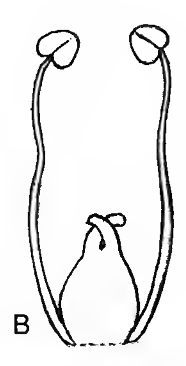
Superficially, the inflorescence of *Weinmannia racemosa* appears to have little in common with those of other members of the section. However, its homology can be deduced if some assumptions are made about its evolutionary relationships. Here, we suggest that *W. racemosa* is most closely related to *W. sylvicola* (the only other New Zealand species), and that overlapping forms of these two species can be identified and used to link the unusual inflorescences in *W. racemosa* with those typical of sect. *Leiospermum*.

In *Weinmannia racemosa* there is always a single PI in a medial position and it can consist of either one (Fig. 5C) or two metamers. When two metamers develop the structure appears similar to a common variant of *W. sylvicola* in which there is no lateral PI (Fig. 5A), except that in this case, the apical bud is not aborted. There is thus a continuity in form between *W. racemosa* and *W. sylvicola*, and between *W. sylvicola* and other *Leiosperma*. The fate of the apical bud in *W. racemosa* makes it unique within sect. *Leiospermum* in that vegetative growth can continue from within the inflorescence. This, together with the absence of lateral PIs and the generally lesser number of metamers in any PI, is the reason for the unusual appearance of the inflorescence in *W. racemosa*. The apical bud (of both the PI and the main stem in this case) can be either dormant or commonly not, when it goes on to produce further leaves and PIs (Fig. 5D).

3. Flowers

While basic floral structure is extremely uniform among different species (see Fig. 3A-G), flowers can be morphologically bisexual (with filaments approximately the same length as the gynoecium so that anthers and stigmas are at about the same level, Fig. 6C), male (with long filaments, the anthers far exserted beyond the stigmas, the ovary small and the styles tiny and incurved, Fig. 6B) or female (with short filaments, the ovary often large and the styles far exceeding the stamens, either straight or curving outwards, Fig. 6A). However, there is often a considerable range in the length of the filaments and occasionally they are not clearly long or short, and then the gender of the flowers is equivocal. Usually the anthers are of similar size in male and female flowers, though unusually small anthers are found, for example, in the apparently





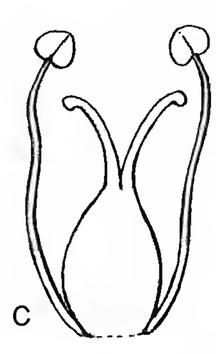


Fig. 6.—Androecium and gynoecium from morphologically female (A), male (B) and bisexual (C) flowers of ***Weinmannia***.—Drawn by J. LEMEUX.

bisexual flowers of *W. fraxinea* from the Solomons.

There is only preliminary information on the functional potential of flowers of different morphological types. In *W. denhamii* Seem. from Vanuatu, the anthers of both male and female flowers contain pollen, although in the female flowers it appears to be less well formed (R.D. HOOGLAND in litt. to J. FLORENCE, 19 May 1987). In *W. parviflora* from Tahiti, no pollen was found in the anthers of morphologically female flowers (*Florence 9089, 9091*), while the anthers of morphologically males ones (*Florence 9089, 9090*) did contain pollen (R.D. HOOGLAND unpublished notes).

Sexual expression and breeding system. In many species, all the flowers on one herbarium specimen, which might contain several inflorescences each composed of several racemes, are of the same morphological type and there is no evidence to suggest that some species are not either simply dioecious (e.g. *W. hutchinsonii, W. luzoniensis* S. Vidal, *W. aphanoneura* Airy Shaw) or hermaphroditic (e.g. *W. serrata* and other species from New Caledonia, *W. racemosa* and *W. sylvicola* from New Zealand, *W. furfuracea* H.C. Hopkins and *W. descombesiana* from Sulawesi).

The expression of sex is more complex in some other species. For instance, a number are polygamodioecious (SMITH 1952), with male and female flowers on separate plants and some bisexual flowers, usually on staminate plants in this case (e.g. numerous species from small Pacific islands). In these species, bisexual flowers are usually less common than unisexual ones, and they may either be mixed in the same inflorescence as the male flowers or in separate but contemporaneous inflorescences. In some species (e.g. *W. marquesana, W. denhamii, W. rapensis*) there are also temporal changes in gender, with cycles of different sorts of flowers on one plant, indicated by the presence of male flowers at anthesis and mature fruits (usually from bisexual flowers) in separate inflorescences. Temporally labile species may contain some stable individuals and others that change gender within and between seasons.

In some predominantly dioecious species (e.g. *Weinmannia urdanetensis*) a few individuals appear to be monoecious. The most complex pattern is seen in *W. fraxinea* where the sexual system varies geographically and some populations may perhaps be apomictic. Better description of the more complex sexual systems clearly requires detailed, long-term field studies.

Compatibility mechanisms have not been studied. There is circumstantial evidence of interspecific hybridization, e.g. in central Viti Levu, where small, infertile roadside plants showed a wide range of vegetative characters, and were likely to have been hybrids between *W. richii* (sect. *Fasciculata*) and *W. affinis* (sect. *Leiospermum*) (HOPKINS & BRADFORD pers. obs.).

Floral biology and pollination. The flowers of *Weinmannia* are massed together in fairly dense, spike-like inflorescences that are arranged around the periphery of the crown, projecting upwards

(Fig. 2C). Individual flowers are bowl-shaped with the anthers and stigmas readily accessible to potential pollen vectors that land on the racemes (i.e. non-restrictive). The flowers are usually white or cream, sometimes pink, and described as scented or not. Nectar is produced in *Weinmannia racemosa* (THOMPSON cited in WARDLE 1966) although none was seen in *W. fraxinea* or *W. affinis* (HOPKINS & BRADFORD pers. obs.). The disc lobes are pale and inconspicuous in *W. fraxinea* in Borneo while in *W. affinis* and *W. vitiensis* in Fiji, they are dark and contrast strongly with the pale corolla. There have been no detailed studies of pollination but bees are probably the main pollen vectors. The flowers of *W. racemosa* in New Zealand are visited by insects including bees, and by the Parsonbird or "*tui*", *Prosthemadera novaeseelandiae* (WARDLE 1966). Racemes of *Weinmannia* also attract a variety of flies and beetles (pers. obs.). A high proportion of female or bisexual flowers on any raceme produces fruit.

4. Fruits and seeds

The capsules (Fig. 2E; 3K,L) are remarkably uniform, with only minor variation between species in size and indumentum. Variation in the persistence of the calyx lobes has been used as a taxonomic character but is variable in a few species. In sect. *Leiospermum*, there is a well developed persistent central column (GODLEY 1983; Fig. 3L) from which the lateral wings of the endocarp separate on dehiscence. In sect. *Fasciculata*, this column is often more weakly developed, or shorter or absent, when the tissue that otherwise forms the column remains attached to the endocarpic fringes of the valves. The capsules are usually referred to as septicidal, but the presence of a free central column after dehiscence means that they are septifragal (see SPJUT 1994).

The seeds are small and the surface of the testa has a complex pattern of sculpturing (DICKISON 1984; WEBB & SIMPSON 1991; Fig. 3H). In most species there is a tuft of comose hairs at each end, although in a few, there are short hairs widely distributed over the entire surface. There is some variation in the length and texture of the comose hairs which appears to affect the length of time the seeds are retained within the capsule after dehiscence, and this may affect their dispersability.

Dispersal. The seeds are probably wind-dispersed (e.g. WARDLE 1966; HOPKINS & BRADFORD pers. obs. in Fiji) although exozoochory has been suggested (GUPPY in FLORENCE 1982: 32, for *Weinmannia parviflora*), the hairs on the seeds perhaps sticking to birds' feathers. Long-distance dispersal must be reasonably effective since the genus has reached many volcanic islands in the South Pacific.

5. Field characters

Life form is rather plastic in some species which can be trees, shrubs, dwarf shrubs and occasionally woody epiphytes, depending upon the vegetation type, altitude and exposure. Bark is often variable within species, and rarely distinctive. Inner bark is often pinkish, brown or reddish brown. Sap wood is white, straw, pinkish, sometimes orange-brown, sometimes turning purple; medium to hard. Heart wood is pink-cream to red or yellow-brown. Young stems and leaves are often conspicuously red (Fig. 2A), mature leaves often darkish green above, shiny; old leaves sometimes turning bright red. Inflorescence axes are sometimes reddish. Flower buds are light green to pink or red. Flowers are creamy white to pink (Fig. 2C,D), rarely light green or purple (*W. purpurea*), often with a slight sweet fragrance; the calyx is pale green, yellowish green or reddish; the corolla and filaments are usually white; the anthers pinkish, cream or straw; the disc yellow-orange or dark red-purple; the ovary light green or pinkish; the styles are pink at the base and the stigmas are white to brown or purplish. Young fruits are greenish, pink or reddish (Fig. 2B,F), turning crimson or rarely purplish green at maturity; dehisced capsules are brown (Fig. 2E).

WEINMANNIA L.

Syst. Nat., ed. 10, 2: 997, 1005, 1367 (1759), nom. cons.; Juss., Gen. Pl.: 309 (1789); Lam., Tabl. Encycl. 1 2, t. 313 (1793); Willd., Sp. Pl., ed. 4, 2: 296, 436 (1799); Benth. & Hook. f., Gen. Pl. 1: 653 (1865); Engl., Linnaea 36: 592 (1870); Engl., in C. Mart., Fl. Bras. 14 (2): 156 (1871); Engl., Nat. Pflanzenfam.,

III, 2a: 101 (1891), ed. 2, 18a: 250 (1930); Baill., Hist. Pl. 3: 373, 447 (1871); Bader, Nova Acta Leop. 23 (148): 170, 430 (1960); Bernardi, Candollea 17: 123 (1961), 18: 285 (1963); Bernardi, Adansonia, ser. 2, 3: 404 (1963); Bernardi Bot. Jahrb. Syst. 83: 126, 185 (1964); Bernardi, in Humbert, Fl. Madag., fam. 93: 3 (1965); Hutch., Gen. Fl. Pl. Dicot. 2: 9 (1967).

Windmannia P. Browne, Civ. Nat. Hist. Jamaica: 212 (1756), nom rejic.; Kuntze, Revis. Gen. Pl. 1: 228 (1891).

Arnoldia Blume, Bijdr. Fl. Ned. Ind.: 868 (1826), non Cass. (1824).

Leiospermum D. Don, Edinburgh New Philos. J. 9: 91 (1830).

Pterophylla D. Don, Edinburgh New Philos. J. 9: 93 (1830).

Ornithrophus Bojer ex Engl., Linnaea 36: 636 (1870), pro syn.

TYPE.—*Weinmannia pinnata* L. from Central and South America and the Antilles.

Generic description of *Weinmannia* in Malesia and the Pacific

Trees or shrubs, rarely epiphytes and perhaps rarely stranglers. Branching sometimes dichotomous in some species, usually so in a minority of species; shoots sometimes slightly thickened or flattened at nodes, internodes terete, the bark finely grooved; pale lenticels often prominent. Indumentum of simple hairs, variable in amount and distribution. Interpetiolar stipules 2 per node, elliptical, ovate, orbicular to subreniform, often with minute adpressed hairs, apex rounded or pointed, margin entire or toothed, a pair of opposite stipules often salverform in juvenile foliage, sometimes caducous in adult foliage, the bases leaving a prominent annular scar around stem at each node after abscission. Colleters purple-red, minute (< 0.1 mm long), frequent at nodes and visible after stipules have fallen, non-functional? Axillary and apical buds covered by a pair of velutinous or sericeous stipules (bud scales). Leaves opposite and decussate, simple (unifoliolate?), trifoliolate or imparipinnate (rarely paripinnate), usually petiolate; petiole and rachis terete, caniculate, or semiterete and flattened on adaxial side, sometimes narrowly winged, especially distally towards the point of insertion of each pair of leaflets; leaflets chartaceous to coriaceous; lateral leaflets often asymmetrical at base, often smaller proximally in a given leaf; margin toothed or crenulate, the crenations acroscopic, margin usually minutely thickened and minutely revolute; secondary veins usually arcuate, branching before reaching margin, one branch arching towards apex and the other towards base to join with tertiary veins arising from a more proximal secondary vein; blade sometimes black-dotted below, sometimes pustulate.

Inflorescence composed of racemes, usually arranged in groups on a sterile axis on which leaf development is partially or wholly suppressed, to form a developmentally integrated unit, rarely not part of such a unit and arising directly from axillary buds on the main leaf-bearing stem; partial inflorescences either axillary or terminal or a combination. Racemes up to 12 cm long with up to 100 or more flowers, the basal part usually bare; axis of raceme longitudinally ridged and often minutely hairy (hairs < 0.1 mm long), sometimes densely so. Floral buds inserted on the axis of the racemes either singly or in small fascicles, each bud or fascicle subtended by a bract; bract often carinate, often histute on abaxial surface, often caducous. Flowers small, unisexual or bisexual, hypogynous or somewhat perigynous, perianth and androecium 4-merous or rarely a few flowers per raceme 5-merous (commonly 5-merous in some areas outside this region); pedicel usually filiform, often minutely hairy (hairs < 0.1 mm long); calyx of 4 lobes, imbricate in bud, ± triangular, attached at their base to the hypanthium at the point of their greatest width, apex broadly acute or somewhat rounded, glabrous or hirsute on outer surface, slightly fleshy; corolla of 4 free petals, not caducous (in this region), usually elliptical, ovate or obovate, constricted at the base (attachment 0.1-0.2 mm across), apex rounded or irregularly emarginate, membranous, sometimes minutely ciliolate; androecium of 8 stamens, obdiplostemonous, the filaments filiform, inserted in a single whorl but alternate ones elongating asynchronously; anthers apiculate, versatile, dehiscing longitudinally, the valves of each thecum unequal; disc of 8 free lobes, alternating with the filaments, usually ± oblong, obcuneate or slightly claviform, sometimes broadly oblong with flanges on either side so that lobes almost form a

continuous ring of tissue, glabrous; gynoecium of 2 (rarely 3) carpels fused at the level of the ovary; ovary ovoid, glabrous to densely hirsute, the hairs drying white; locules 2(-3); styles 2(-3), free, awl-shaped, glabrous except occasionally at the base, conduplicate and furrowed on adaxial side; stigmas terminal, small or sometimes capitate, papillose; ovules ca. 8-16 per locule, placenration axile.

Fruit small (< 6 mm long), a septicidal or usually septifragal capsule dehiscing from the apex into 2 parts which remain attached to the receptacle at their base to form a cup-shaped structure wirh the styles usually persistent at the apex; the valves composed of 2 layers: exocarp dark brown, pubescent, strigose or glabrous, smooth or minutely ridged; endocarp yellow, smooth, with minute transverse sculpturing on concave surface, usually completely adnate to exocarp or sometimes partially free especially towards the apex, the septum separating the locules extending as wing-like projections on either side of the exocarp at dehiscence; free central column formed from placenta often present and sometimes persisting after the valves have fallen; receptacle sometimes saucer-like at base; calyx lobes persistent or not; corolla and disc lobes occasionally persistent. Seeds small (< 1 mm long), elliptical in outline and circular in transverse section, generally 2 × as long as broad when fully mature, the surface minutely sculptured, raphe sometimes visible as a minute ridge, usually comose with straw-like hairs in a tuft at each end, sometimes hairs arising ± all over the surface, longer at the ends.

About 40 species in Malesia and the Pacific, belonging to two sections.

1. Sect. *Fasciculata* Bernardi ex Hoogland & H.C. Hopkins, **sect. nov.**

Sect. *Fasciulatae* Bernardi, Bot. Jahrb. Syst. 83: 132, 158 (1964), nom. inval., sine typus.

TYPE (here designated).—*Weinmannia fraxinea* (D. Don) Miq.

Flowers pedicellate and inserted on the axes of the racemes entirely or largely in fascicles, i.e. several pedicels arising in a group, the group subtended by a single small bract (Fig. 3P), rarely inserted singly (*W. descombesiana*). Inflorescence composed of 1-3 opposite pairs of partial inflorescences inserted in series in the axils of the most distal pairs of leaves; each partial inflorescence consisting of a single metamer, which comprises a sterile peduncle and 2 or 4 racemes inserted at its distal end (to form a "dyad" or a "tetrad", see Fig. 4A,B); leaves at nodes from which racemes arise usually totally suppressed; stipules not usually present at nodes within partial inflorescences; "collars" around peduncles of partial inflorescences absent; bud within each partial inflorescence, at apex of peduncle between the central racemes, present and usually dormant during flowering; apical bud of main stem, between central peduncles, present and usually dormant during flowering; buds lateral to axillary buds at most distal leaf-bearing node (lateral auxiliary buds) absent.

Stipules often ± orbicular. Branching not dichotomous. Leaf blades not punctate below.

Capsules ± smooth and not ridged; indumentum on valves softly pubescent; after dehiscence, central column weakly developed; calyx lobes often but not always persistent in fruit.

20 species in Malesia and the western Pacific, extending as far east as Fiji.

2. Sect. *Leiospermum* (D. Don) Engl., Nat. Pflanzenfam. III 2a: 101 (1891), ed. 2, 18a: 256 (1930).

Sect. *Racemosae* Bernardi, Bot. Jahrb. Syst. 83: 132, 185 (1964), nom. superfl. et sine typus.

TYPE.—*Weinmannia racemosa* L. f.

Flowers pedicellate and inserted on the axes of the racemes singly, i.e. each pedicel arising in the axil of a small bract (Fig. 3N). Inflorescence composed 1-3(-5) partial inflorescences, usually inserted medially and laterally; lateral PIs usually consisting of one metamer [dyad (Fig. 4H,K) or triad (Fig. 4F,L)]; sometimes lacking the basal

sterile stem section in *W. parviflora*); medial PIs consisting of one metamer (dyad or triad), two metamers [tetrad (Fig. 5A) or pentad (Fig. 4G)] or three metamers (heptad); apical bud of shoot usually fertile (developing into a raceme in triads, pentads and heptads), sometimes aborted (in dyads and tetrads) or rarely dormant or vegetative (e.g. *W. racemosa*, Fig. 5C,D); leaves at nodes from which racemes arise not suppressed, partially suppressed or totally supptessed; stipules sometimes present at nodes within partial inflorescences; "collars" around peduncles of lateral partial inflorescences often present (Fig. 3M); apical buds within each lateral PI either developed into a medial raceme or aborted; lateral auxiliary buds (i.e. lateral to axillary buds) present at most distal leaf-bearing node and often at other nodes also.

Stipules often ligulate, elliptical or ovate, the apex rounded or pointed. Branching sometimes dichotomous. Leaf blades often punctate below.

Capsules often minutely ridged; indumentum on valves strigose or absent; after dehiscence, central column usually well developed and persistent; calyx lobes often falling in fruit.

There are 17-19 species in the Pacific, extending westwards to Papua New Guinea (Bismarck Archipelago and Karkar Island).

Notes on the species accounts

1. Vegetative characters. Because of variability in the leaves depending their position, even within the crown of one tree, and on the age of the plant, only leaves from fertile shoots are described. Dimensions given are for the largest leaves per specimen. Characters for juvenile or coppice shoots are given separately where known. Terminology for the indumentum follows HEWSON (1988).

2. Inflorescence. The most frequent structures are described but not all variants.

3. Flowers. The insertion of the pedicels on the axes of the racemes is scored in bud where possible as this is sometimes less clear after the flowers have opened and the bracts have fallen. The length of pedicels is given for flowers at anthesis and may be slightly longer in the fruiting stage. The length of the calyx lobes is measured from their point of attachment to the receptacle to their apex (Fig. 3E). The length of the style includes the stigma.

4. Breeding system. Species are described as hermaphroditic, dioecious or polygamodioecious based on the morphology of the flowers (Fig. 6). The reproductive potential of flowers of different sorts has not been investigated.

5. Field characters. Many field characters are common across the genus and are not always repeated in each species account.

6. Types. In species accounts for which HCFH is the sole author, ! is used to indicate type specimens that have been studied. Collection details for types are not usually repeated in the list of material examined.

7. Specimen citations. For those species where I have seen relatively few collections, all material examined is listed. For those where there is much more material, a selection is cited to illustrate the morphological and geographical range of the species.

8. Abbreviations used in citations of specimens. Gn. = Gunung (mountain), Bt. = Bukit (hill), Mt. = mountain, Isls. = island, Kamp. = kampong (village), R. = river, Rd. = road, Sg. = Sungai (stream or small river); juv. = juvenile, fl. = flowers, fr. = fruits, yfr. = young fruits, st. = sterile; N = north, S = south, C = central, nr. = near, ft. = feet, Distt. = District, Prov. = Province, Div. = Division, Ond. afd. = Onderafdeling (subdivision).

Five species are recognised from western Malesia, the Lesser Sunda Islands and the Moluccas, all belonging to sect. *Fasciculata*. *Weinmannia fraxinea* is widespread and variable, and considerably more than half the collections from Malesia belong to this species. *Weinmannia clemenisae* is endemic to stunted forest on ultramafic soils on Mt. Kinabalu in Borneo, *W. aphanoneura* occurs in Borneo and Sumatra, and *W. hooglandii* is from high altitude in Peninsular Malaysia. *Weinmannia furfuracea* is known from this region by a single specimen from Seram (*Rutten 2231*) and is described with the other species which occur in Sulawesi, in Part 2 (HOPKINS 1998a).

Key to the species of the Malay Peninsula, Greater and Lesser Sunda Islands and Moluccas

1. Indumentum on young stems, leaf rachises, inflorescence axes and lower surface of leaflets red-brown, often scurfy; apex of lateral leaflets obtuse (Seram) .... **5. W. furfuracea (see p. 49)**
1'. Indumentum on young stems, leaf rachises, inflorescence axes and lower surface of leaflets grey to golden brown, puberulent to tomentose, not scurfy; apex of lateral leaflets acuminate, acute or obtuse 2
2. Lateral leaflets small, 1.4-2.7 × 0.5-1 cm, boat-shaped or ± oblong; young shoots tomentose-velutinous 3
2'. Lateral leaflets larger (2.2-)4.2-8.5(-12) × (0.8-)1.2-3.5(-4.5) cm, lanceolate, elliptical, narrowly obovate to ovate; young shoots ± glabrous, puberulent or tomentose 4
3. Leaflets bullate and the margin strongly recurved so leaflet is boat-shaped; lateral leaflets 6-13 pairs per leaf (Mt. Kinabalu, Sabah) .... **2. W. clemensiae**
3'. Leaflets flat, not bullate and the margin flat or minutely revolute; lateral leaflets 4-8 pairs per leaf (Peninsular Malaysia) .... **4. W. hooglandii**
4. Lateral leaflets narrowly elliptical to narrowly obovate, the base cuneate, the apex acute to obtuse, drying chestnut-brown, 1-4 pairs per leaf; leaf rachis sometimes narrowly winged; inflorescence of 1-2 pairs of dyads ....**3. W. aphanoneura**
4'. Lateral leaflets, lanceolate, elliptical or ovate, not obovate, the base usually unequal and varying from cuneate to rounded, the apex narrowly acute to acuminate, usually drying greenish-brown, 1-8 pairs per leaf; leaf rachis terete, not winged; inflorescence of 1-3 pairs of dyads or tetrads .... **1. W. fraxinea**

1. Weinmannia fraxinea (D. Don) Miq.

Fl. Ned. Ind. 1(1): 718 (1856); [Sm. ex D. Don, Edinburgh New. Philos. J. 9: 93 (1830) pro syn.]; Engl., Linnaea 36: 644 (1870), Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Scheff., Nat. Tijdschr. Ned. Ind. Batavia 34: 40 (1874); Pamp., Ann. Bot. (Rome) 2: 89 (1905); Merr., Interpr. Herb. Amboin.: 244 (1917); Bernardi, Bot. Jahrb. Syst. 83: 167 (1964).—*Pterophylla fraxinea* D. Don, Edinburgh New Philos. J. 9: 93 (1830); Walp., Repert. Bot. Syst. 2: 374 (1843), 5: 834 (1846); Müll. Berol., in Walp., Ann. Bot. Syst. 5: 31 (1858).—*Windmannia fraxinea* (D. Don) Kuntze, Revis. Gen. Pl. 1: 228 (1891).—Type: *C. Smith s.n.* (Moluccas), Honimoa, Apr. 1797 (holo-, LINN-SM!).

Arnoldia heterophylla Blume, Bijdr. Fl. Ned. Ind.: 869 (1826); DC., Prodr. 4: 12 (1830); G. Don, Gen. Hist. 3: 201 (1834); D. Dietr., Syn. Pl. 2: 1313 (1840); non *Weinmannia heterophylla* Kunth (1823).—*Weinmannia sundana* Miq., Fl. Ned. Ind. 1 (1): 718 (1856); Engl., Linnaea 36: 639 (1870), Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Scheff., Nat. Tijdschr. Ned. Ind. Batavia 34: 38 (1874); Koord. & Valeton, Bijdr. Boomsoort. Java: 403 (1900); Backer, Schoolfl. Java: 472 (1911); de Wit, Rumphius Memorial vol.: 411 (1959).—*Windmannia sundana* (Miq.) Kuntze, Revis. Gen. Pl. 1: 228 (1891).—Type ("in Javae sylvis montanis prov. Batam", probably in error): lecto-, here designated, chosen by HOOGLAND, *Reinwardt s.n.*, Amboina, July 1821, L! [Herb. Ludg. Bat. 908.239-...452].

Spiraea pinnata Blume, Catalalogus: 76 (1823); Nees, Flora 8: 148 (1825); non Moench. (1794).—*Arnoldia pinnata* Blume, Bijdr. Fl. Ned. Ind. (15): 868 (1826); DC., Prodr. 4: 12 (1830); G. Don, Gen. Hist. 3: 201 (1834); Hassk., Pl. Jav. Rar.: 324 (1848); Blume, Flora 41: 254 (1858); non *Weinmannia pinnata* L. (1759).—*Weinmannia blumei* Planch., Lond. J. Bot. 6: 470 (1847); Miq., Fl. Ned. Ind. 1 (1): 718 (1856); Engl., Linnaea 36: 640 (1870), Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Scheff., Nat. Tijdschr. Ned. Ind. Batavia 34: 39 (1874); King, Mat. Fl. Malay Penins. 9: 299 (1897); Koord. & Valeton, Bijdr. Boomsoort. Java: 399 (1900); Pamp., Ann. Bot. (Rome) 2: 89 (1905); Koord.-Schum., Syst. Verz. 1, Fam. 120: 4 (1913); Backer, Schoolfl. Java: 472 (1911); Koord., Exkurs.-Fl. Java: 311 (1911); Koord. & Valeton, Atlas Baumart. Java 1: t. 200 (1913); Ridl., Fl. Malay. Penins. 1: 682 (1922); Corner, Wayside Trees Malaya 1: 201, t. 52 (ed. 1, 1940; ed. 2, 1952), 1: 224, t. 55 (ed. 3, 1988); Backer & Bakh. f., Fl. Java 1: 506 (1963); Bernardi, Bot. Jahrb. Syst. 83: 161 (1964); Whitmore, Guide For. Brit. Sol. Isl.: 59, 133, 152, 206 (1966); Steenis, Mount. Fl. Java: t. 13, fig. 7 (1972); Whitmore, Tree Fl. Malaya 1: 179 (1972).—*Weinmannia arnoldia* A. Gray, U.S. Expl. Exped., Phan. 1: 675 (1854).—*Windmannia blumei* (Planch.) Kuntze, Revis. Gen. Pl. 1: 228 (1891).—Type (Crescit in sylvis montanis Javae insulae): lecto-, here designated, chosen by HOOGLAND, *Blume 816a*, L! [Herb. Ludg. Bat. 908.238-...539]; *syn. nov.*

Weinmannia horsfieldii Miq., Fl. Ned. Ind. 1(1): 718 (1856); Engl., Linnaea 36: 642 (1870); Scheff., Nat. Tijdschr. Ned. Ind. Batavia: 39 (1874).—*Windmannia horsfieldii* (Miq.) Kuntze, Revis. Gen. Pl. 1: 228 (1891).—Type (Java, bij Soerabaja, door Horsfield ontdekt): *Horsfield s.n.* (holo-, BM!); *syn. nov.*

Arnoldia fraxinifolia Blume, Flora 41: 254 (1858);

Müll. Berol., in Walp., Ann. Bot. Syst. 5: 31 (1858).—*Weinmannia fraxinifolia* (Blume) Miq., Fl. Ned. Ind. 1(1): 1095 (1858); Engl., Nat. Pflanzenfam., ed. 2, 18a: 255 (1930).—Type (In sylvis elatioribus Javae occidentalis): lecto-, here designated, chosen by HOOGLAND, *Blume s.n.*, Java, in cacumine montis, Malabar, L! [Herb. Ludg. Bat. 908.238-...577 & 908.238-...578]; *syn. nov.*

Weinmannia papuana Schltr., Bot. Jahrb. Syst. 52: 162 (1914); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930).—Type: *Ledermann 9784*, North East New Guinea, in dense humid forest on the April River, 200-400 m, Nov. 1912 (holo-, B; iso-, L!); *syn. nov.*

Weinmannia ledermannii Schltr., Bot. Jahrb. Syst 52: 162 (1914); Lane-Poole, Rep. For. Res. Terr. Papua New Guinea: 63, 90, 91 (1925); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); L.M. Perry, J. Arnold Arbor. 30: 160 (1949).—Type: *Ledermann 9922*, North East New Guinea, in montane forest on Lordberge, ca. 1000 m, Nov. 1912 (holo-, B; iso-, K!, L!); *syn. nov.*

Weinmannia tomentella Schltr., Bot. Jahrb. Syst. 52: 163 (1914); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); *Bernardi*, Bot. Jahrb. Syst. 83: 179, t. 28 (1964).—Type: *Ledermann 8172* (not 8173 as given by SCHLECHTER [1914]), North East New Guinea, in forest at foot of Hunstein peak, 200-400 m, Aug. 1912 (holo-, B!); *syn. nov.*

Weinmannia blumei Planch. var. *major* Ridl., Fl. Malay. Penins. 5: 307 (1925).—Type: *Ridley 16029*, Malay Peninsula, Pahang, Gunong Tahan, ca. 5500 ft., July 1911 (lecto-, here designated, chosen by HOOGLAND, SING!; isolecto-, BM!, K!, SING!); *syn. nov.*

Weinmannia dictyoneura Schltr., Bot. Jahrb. Syst. 52: 163 (1914), non Diels (1906).—*Weinmannia alta* Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Bernardi, Bot. Jahrb. Syst. 83: 160 (1964).—Type: *Ledermann 10129*, North East New Guinea, in montane forest on Lordberge, ca. 1000 m, Dec. 1912 (holo-, B; iso-, K!); *syn. nov.*

Weinmannia borneensis Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Airy Shaw, Bull. Misc. Inform. 1940: 259 (1940); Heine, Mitt. Bot. Staatssamml. München 1: 212 (1953); Bernardi, Bot. Jahrb. Syst. 83: 164, t. 17 (1964).—Type: *Native Collector 722*, Sarawak, s.loc., s.d. [fide specimen in PNH: road to summit of Gunong Matang, 12 Aug. 1911, leg. *Dabong*] (holo-, B; iso-, BM!, BO!, K!, L!, PNH); *syn. nov.*

Weinmannia dulitensis Airy Shaw, Bull. Misc. Inform. 1940: 259 (1940).—Type: *Native Collector 1671*, Sarawak, Dulit Ridge, forest nr. waterfall, ca. 1200 m, 10 Sep. 1932 (holo-, K!; iso-, L!, SING!); *syn. nov.*

Weinmannia hypoglauca Kaneh. & Hatus., Bot. Mag. (Tokyo) 56: 111, t. 7 (1942).—Type: *Kanehira & Hatusima 12797* (Irian Jaya), Boemi, 40 km inward of Nabire, 400 m, 11 Mar. 1940 (holo-, FU, photo at K!; iso-, BO!, L!); *syn. nov.*

Cortex papetarius Rumph., Herb. Amboin. 3: 212, t. 137 (1743), nom. illeg.

Small to large tree, up to 25(-40) m high. Young stems puberulent to tomentose, rarely glabrous, older stems glabrescent with numerous lenticels; branching not usually dichotomous. Stipules often caducous, ± orbicular to subreniform to broadly spathulate, 0.8 × 0.8 to 1.5 × 1.8 cm, narrowed at base, apex broadly rounded, abaxial surface shortly strigose especially towards base, adaxial surface glabrous. Leaves imparipinnate, with (0-)1-8 pairs of lateral leaflets, total length 5.5-15.5 cm including petiole of 1-3 cm; rachis segments 1-2.5 cm long; petiole and rachis segments terete, indumentum varying from glabrous to tomentose-velutinous on adaxial side or abaxial side or both; lateral leaflets ± sessile, usually broader towards the base, varying from lanceolate to narrowly elliptical to narrowly ovate to ovate, the largest per leaf (2.2-)4.2-8.5(-12) × (0.8-)1.2-3.5(-4.5) cm, proximal leaflets usually smaller than more distal ones, base frequently unequal to dimidiatus, rounded to cuneate on either side, apex acute to acuminate; terminal leaflet narrowly elliptical to narrowly ovate, 2.5-10 × 1-3.3 cm including petiolule of 0.3-1.5 cm, blade ± same size as largest lateral leaflets or larger, base attenuate into petiolule, apex acuminate; blades chartaceous to subcoriaceous, glabrous, not punctate below; margin crenate, 8-14 notches on each side in the lateral leaflets, crenations rounded and acroscopic or triangular and not acroscopic; midrib prominent and shortly hirsute below, indented above and sometimes hirsute towards base; secondary and tertiary veins ± flat above and minutely prominent below, sometimes drying paler than intervenium.

Inflorescence 1-3 opposite pairs of lateral dyads or tetrads at most distal node of main stem, inserted in series when > 1 pair; apical bud of the main stem between the peduncles of the central dyads densely sericeous; bud at apex of peduncles in angle between the racemes sericeous; sometimes a few successive nodes on one shoot producing partial inflorescences simultaneously; peduncles 0.3-1.8 cm long; racemes 7.5-15 cm

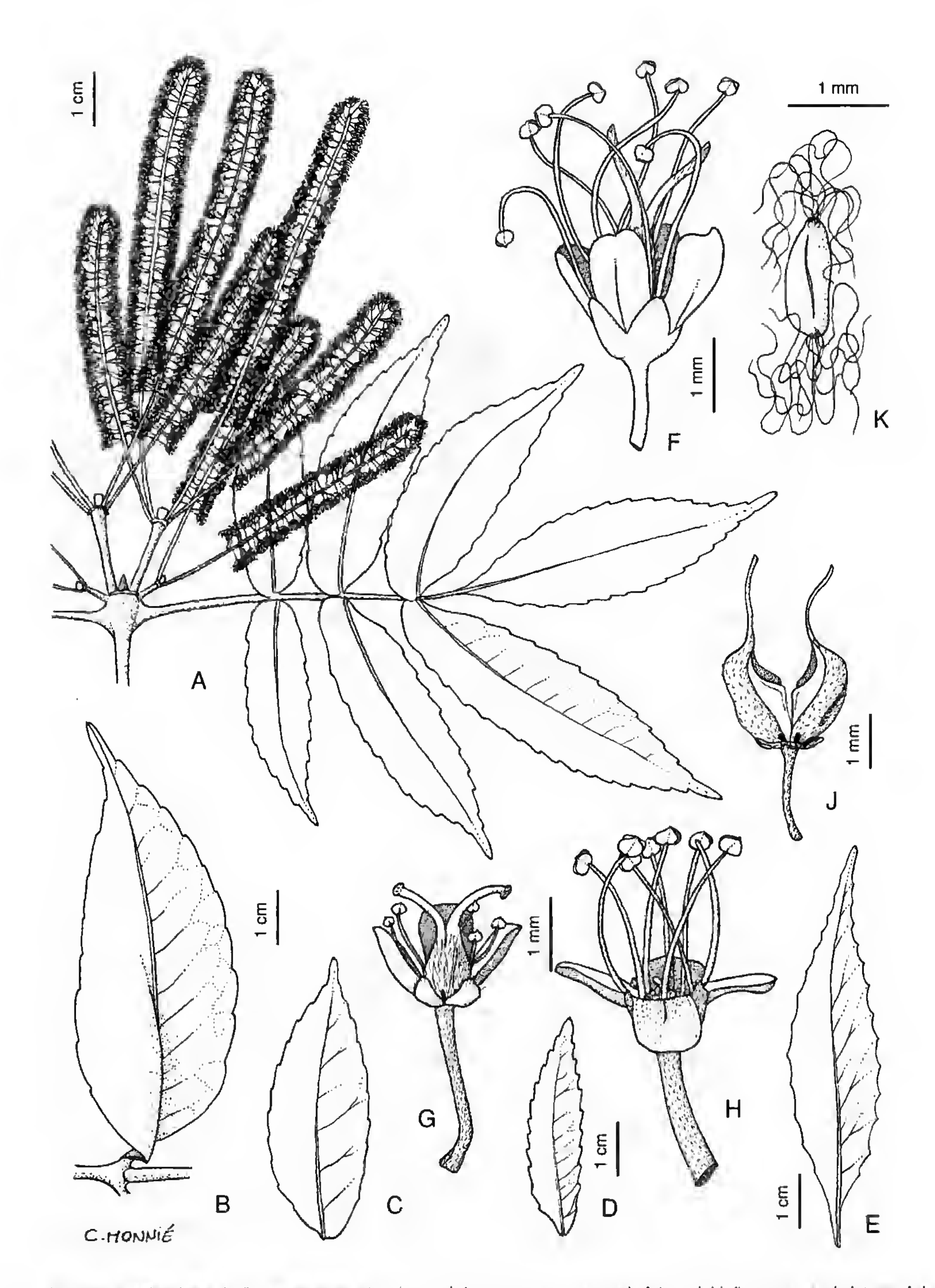


Fig. 7.—***Weinmannia fraxinea***: **A**, flowering shoot showing an inflorescence composed of 4 partial inflorescences (mixture of dyads and tetrads); note dormant apical bud and buds within each partial inflorescence; **B**, lateral leaflet, typical of *W. fraxinea "dulitensis"*; **C**, lateral leaflet, typical of *W. fraxinea "borneensis"*; **D**, lateral leaflet, typical of *"blumei"*; **E**, lateral leaflet, typical of *W. fraxinea* from the Moluccas; **F**, bisexual flower; **G**, female flower, one petal removed; **H**, male flower; **J**, dehisced capsule, central column not evident; **K**, seed. (A, *Hopkins & Bradford 5006*; B, *Hopkins & Bradford 5013*; C, *Meijer SAN 22106*; D, *Nousjet 670*; E, *Kuswata & Soepadmo 250*; F, J, K, *Dickison 215*; G, *Geesink 8953*; H, *Hopkins & Bradford 5006*).—Drawn by C. MONNIÉ.

long; peduncles and axes of racemes minutely puberulent to tomentose. Floral buds inserted in fascicles; floral bracts ligulate-carinate 0.5-1 mm long, caducous, with short flattened hairs. Flowers unisexual or bisexual; pedicel (1.1-)1.5-3 mm long, minutely hairy; calyx lobes triangular, 0.6-0.9 mm long, hirsute at base; petals oblong to obovate, 1.1-1.8 × 0.7-1.2 mm, apex rounded or rarely emarginate, ciliolate or not; disc lobes free, oblong, 0.2-0.5 mm long, or rarely forming an almost complete disc; in male flowers: filaments ca. 2.9 mm long, anthers ca. 0.5 mm long, ovary ca. 0.5 mm, densely pubescent, styles 0.1 mm, incurved; in female flowers: filaments 0.6-1.2 mm long, anthers 0.3 mm long, ovary 0.6-1.2 mm long, densely pubescent, styles 1-1.3 mm long, straight; in bisexual flowers: filaments 3-3.5 mm long, ovary 0.6-0.8 mm long, pubescent, styles 1.5-2 mm long.

Capsules (2-)2.5-4(-6) × 1.5-2(-3.1) mm at dehiscence, plus styles 1-2 mm long, the exocarp pubescent; calyx lobes usually persistent; central column weakly developed. Seeds 0.8-1.1 mm long, comose at both ends, the hairs up to 2 mm long.—Fig. 2A,C,D; 7A-K; 8.

Juvenile foliage.—Small seedlings have 3-5 pairs of chartaceous leaflets tinged with red, the margin dentate and the teeth acroscopic; the stipules are persistent, ± round and often toothed (*Hopkins & Bradford 5017*, Borneo). Older seedlings have up to 12 pairs of leaflets with similar margins and the stipules are again often persistent and toothed (*Hopkins & Bradford 5003*, Borneo; *Verheijen 4397*, Flores; *Steenis 7398*, Java *p.p.*). Indumentum on the main stem and leaf rachises varies from almost glabrous to tomentose.

Table 1.—The number of herbarium specimens with flowers of different morphological types, as determined by the relative lengths of the styles and filaments, in *Weinmannia fraxinea* from various regions and two closely related species. Sex of flowers was determined at anthesis (columns 2-4) or rarely in fruit (column 5) but never prior to elongation of the filaments.

Geographical region	Male flowers	Bisexual flowers	Female flowers	Fruit with remnants of tiny stamens (i.e. from female flowers)	Breeding system (as indicated by morphology of flowers)
Sumatra	9	0	9	0	dioecious
Malay Peninsula	15	1	9	3	largely dioecious
Java	19	1 + 3 (male + bisexual)	16	0	polygamodioecious
Borneo	7	4	9	0	partly dioecious
Lesser Sunda Islands	4	0	2	0	dioecious
Moluccas	9	0	10	6	dioecious
New Guinea	3	21	1	1	largely hermaphroditic
Solomons	0	15	0	0	hermaphroditic
Sulawesi (*W. devogelii*, see part 2, p. 48)	3	0	4	0	dioecious
Vanuatu (*W. macgillivrayi*, see part 3, p. 85)	1	2 (male + bisexual)	1	4	polygamodioecious

BREEDING SYSTEM.—Varying with geography, either dioecious, polygamodioecious or hermaphroditic. See Table 1.

FIELD NOTES.—Small, often shrub-like tree 5-15 m tall at high altitude, to tall, slender tree up to 25(-40) m high × 50 cm dbh at lower altitude. Buttresses usually absent; when present, up to 2 m, concave, rounded. Bark variable but frequently brownish and flaking; varying from dark brown, pink- or orange-brown, greyish, fawn, reddish purple to rich tawny rust, and the texture scaling, fissured, smooth, flaking or rugose-lenticellate. Inner bark variable, often reddish; also orange-yellow, brownish grey, golden-brown or reddish brown and fibrous. Slash wood dirty yellow-white; no exudate. Heart wood light orange to beefy red. Stipules sometimes prominent; young leaves, stems and stipules often pinkish, bright red or purplish. Mature leaves shining above, sometimes with red margins, the rachis brown-red, the stipules light green; old leaves bright red. Flower buds green, yellow, pink or red; inflorescence axes green or dull red; pedicels sometimes red. Flowers white, yellowish, pinkish or pale green; pedicels and calyx greenish or pinkish; petals and filaments white or creamy pink; disc yellowish; anthers white to sulphur; ovary red with styles pink or white, the hairs white; flowers lightly scented or not. Young fruit green, reddish green, yellow, bright red, purplish or red-brown; old fruits blackish; seeds yellowish white.

DISTRIBUTION AND ECOLOGY.—From northern Sumatra eastwards through Malesia (Malay Peninsula, Greater and Lesser Sunda Islands, Moluccas, New Guinea and Bismarck Archipelago) to the Solomon Islands; absent from Sulawesi and the Philippines. (0-)500-2000(-2700) m. In western Malesia, usually from mid to high elevations and more frequent at lower elevations in the eastern part of its range (Malay Peninsula: (450-)1000-2065 m; Sumatra: 500-2700 m; Java: 600-2400 m; Borneo: (0-)500-1970 m; Lesser Sunda Islands: 500-1500+ m; New Guinea: 10-1450(-2250) m; Solomons: 10-620 m).

In western Malesia, at lower elevations in primary and secondary forest, including with *Casuarina*. Locally common small tree above 500 m, in hill forest, often on ridges and spurs or on slopes below ridge top. Varying in abundance from uncommon to one of main constituents of montane forest (e.g. *Jacobs 8201*, Sumatra), sometimes locally common and clumped. At higher altitude found in mossy heath forest, montane rain forest and dwarf, montane scrub and alpine shrubbery. Often on young volcanic soils and open, stony ground, sometimes recently burnt and dominated by ferns. Also grows on soils derived from sandstone, dacite and ultrabasics and recorded from acidic, water-logged sands in *Agathis* forest (*Kostermans 12903*), sandy, kerangas-like soil, and mixed peat swamp forest at sea level (Borneo).

SELECTED COLLECTIONS (from a total of 347 seen for this region).—SUMATRA: ***Aceh***: *Steenis 9543*, Gayo lands, Gn. Kemiri, 1800-2000 m, st., 6 Mar. 1937 (BO); *Wilde & Wilde-Duyfjes 13087*, Gn. Leuser Nat. Res., Gn. Bandahara, track from kamp. Seldok NE to blang S of summit, 25 km NNW of Kutatjane, 1800 m, yfl., 20 June 1972 (K, KEP, L); *Wilde & Wilde-Duyfjes 14151*, Gn. Leuser Nat. Res., Gn. Ketambe, 8-15 km SW from mouth of Lau Ketambe, 40 km NW of Kutatjane, 2000 m, fl., 9 Aug. 1972 (K, KEP, L); *Wilde & Wilde-Duyfjes 16638*, Gn. Leuser Nat. Res., Gn. Mamas, 9 km SW from mouth of Lau Ketambe, 30 km NW of Kutatjane, 1500 m, fl., 6 May 1975 (K, KEP, L). (***Tapanuli***): *Alston 14891*, Baniara, S of Sidikalang, fl., fr., 28 Mar. 1954 (BM, L); *Mareman 6, bb 5261*, Toba plateau, nr. Pansurbatu, 2693 m, fl., 24 Jan. 1923 (BO, L). ***W Sumatra***: *Abid gl. Malin Maradjo 6, bb 18608*, nr. Kerintiji Tengah, 1400 m, st., 20 Mar. 1934 (BO); *Bünnemeyer 908*, NW slope Talaman, Ophir Distr., 1900 m, fl., 28 May 1917 (BO); *Meijer 5218*, Mt. Singgalang nr. Bukittinggi, 2000-2200 m, fl., yfr., 1 July 1956 (L); *Meijer 5898*, Mt. Sago nr. Payakumbuh, 1500 m, yfr., 22 June 1957 (L). (***E coast***): *Bangham & Bangham 1020*, Trail from Medan to top of Sibajak volcano, 4200-6500 ft., fl., 15 Feb. 1932 (K, SING); *Lörzing 7941*, Central Habinsaran, right bank of Kuwal between Parsoburan and Nassau, 850 m, buds, 15 Nov. 1920 (BO, L); *Teysman s.n.*, Lingga, Mt. Tanda, st. (BO, L); *Yates 2007*, Brastagi, 4500 ft., fl., yfr., 12 Mar. 1926 (BO, L, SING). ***Benkulu***: *Mesverip 20, bb 8753*, Kroë, nr. Gn. Kewala, 800 m, st., 7 Mar. 1925 (BO); *Voogd bb 17032*, Lebong, nr. Bt. Daun, 1800 m, st., 1 Apr. 1932 (BO). ***Palembang***: *Steenis 3617*, Gn. Pesagi, N ridge SSE of L. Ranau, 2000 m, st., 4 Nov. 1929 (BO). ***Lampong***: *Jacobs 8201*, Mt. Tanggamus, 5°26'S-104°41'E, 1500 m, fl., 1 May 1968 (A, BISH, K, KEP, L).—PENINSULAR MALAYSIA: ***Kedah***: *Wyatt-Smith KEP 79272*, top of Kedah Peak, 3950 ft., fl., 28 Apr. 1957 (K, KEP, L). ***Perak***: *Ridley 3027*, top of

Gn. Hijau, fl., Mar. 1892 (BM, K, SING); *Wray 3814*, Gn. Babu, Larut, 5000 ft., fr., Mar. 1890 (K, P, SING). ***Kelantan***: *Symington KEP 37700*, Gn. Stang, st., 10 Oct. 1934 (SING). ***Trengganu***: *Cockburn FRI 10828*, E approach ridge Gn. Mandi Angin, 4200 ft., buds, 12 July 1962 (K, KEP, L); *Moysey & Kiah SF 31040*, Gn. Padang, 4000 ft., buds, June 1937 (KEP, SING). ***Selangor***: *Maxwell 78-318*, Genting Highlands, Gn. Ulu Kali, 1700 m, fl., 3 June 1978 (L). ***Pahang***: *Corner SF 33161*, Fraser's Hill, 4000 ft., fl., 10 Aug. 1937 (A, BO, L, SING); *Kloss 126* or *SF 12124*, Gn. Tahan, Padang Sebrang, 4900 ft., fr., 6 July 1923 (SING); *Soepadmo 950*, between Wray's camp and the Padang, Taman Negara, 3000-5000 ft., fl., 4 Sep. 1970 (A, K, L, SAN, SAR); *Symington SF? 36224*, Cameron Highlands, summit of Gn. Terbakar, fr., 12 Apr. 1934 (K, KEP, SING); *Whitmore FRI 3266*, main NE ridge of Gn. Bebom, Krau Game Reserve boundary, 5000 ft., fr., 18 Mar. 1967 (A, K, KEP, L). ***Malacca***: *Griffith 2507*, Gn. Toondot Ledang top, fl., 1861-62 (K, P); *Ridley 3295*, Mt. Ophir, buds, June 1892 (K, SING). ***Johore***: *Mat Asri bin Ngah Sanah FRI 38681*, Gn. Ledang, nr. Telecom building, 450 m, fl., 20 Apr. 1993 (KEP); *Whitmore FRI 12394*, NW Johore, Gn. Ledang (Mt. Ophir), 3700 ft., fl., 17 July 1969 (A, K, KEP, L).—Java (W = west, C = central, E = east): *Arens 79*, E, Malang, Ardjuna, between Kokopan and Lalijiwo, 2400 m, fl., 15 Oct. 1915 (BO, L); *Backer 7118*, W, Bantam, Gn. Aseupan nr. Menes, 400-600 m, fr., 12 Mar. 1913 (BO); *Backer 22969*, W, Bogor, Gn. Beser, nr. Tidadap, S of Tibebet, 1050 m, buds, 10 Sep. 1917 (BO); *Backer 37408*, E, Malang, Pasuruan, Gn. Ardjuna, above Tjeter, 2000 m, fl., 3 Oct. 1927 (L); *Balgooy & Wiriadinata 2913*, W, Nirmala Estate, Gn. Halimun area, 1350 m, fl., 10 June 1980 (A, L); *Boschproefstation 6691*, E, Madiun, Kedunggalar forest, fr., Mar. 1927 (BO); *Burck 483*, W, Priangan, Garut/Karotjok, buds, fr., 4 July 1891 (BO, L); *Hochreutiner 1941*, W, Bogor, Mt. Salak, towards W on Gn. Bundet, 800 m, fl., 2 Oct. 1904 (L); *Junghuhn s.n.*, C, Semarang, Medinie, Ungarang, yfr. (L); *Kalshoven VI*, W, Bogor, Tjiadhu (Gn. Salak), 900 m, fl., Nov. 1918 (BO); *Koorders 7640*, W, Bogor, Tjibodas, Tjiputri, fl., 22 Feb. 1890 (BO, L); *Koorders 7645*, W, Bogor, Takoka, 1100 m, fl., 3 Aug. 1890 (BO, L, P); *Koorders 6746*, W, Priangan, NW Galunggung, nr. top Pangentjongan-Telagabodas, 2229 m, fl., 1 Jan. 1891 (L); *Koorders 7648*, W, Bantam, Gn. Pulasari, Kihudjan, Pandeglang, 1050 m, fr., 13 June 1892 (BO, L); *Koorders 7652*, C, Semarang, Telomjo, Ambarawa, fl., fr., 9 Oct. 1888 (BO, K, L); *Koorders 7653*, C, Banyumas, nr. Pringombo, Bandjarnegara, yfr., 9 Nov. 1891 (BO); *Koorders 7657*, C, Banyumas, Midangan Mts. nr. Pringombo, 700-1000 m, fl., 15 Nov. 1891 (BO, L); *Koorders 12441*, E, Madiun, W Gn. Wilis, Ngebel, 1350 m, yfr., 22 Oct. 1892 (A, BO, L, SING); *Koorders 26546*, W, Priangan, Garut, Wanaradja, Pasir, Pasanggrahan Pangentjongan, fr., 5 Feb. 1897 (BO, L); *Koorders 27952*, C, Semarang, Ambarawa, Telomojo, fl., 13 June 1897 (BO, L); *Koorders 34183*, E, Madiun, Ngebel, Ponorogo, fr., 19 Nov. 1900 (BO, L); *Koorders 37915*, E, Malang, Tengger, 1650 m, fl., 30 Oct. 1899 (BO, K); *Koorders 38229*, E, Malang, Gn. Ardjuno, Pasuruan, 2000 m, fr., 11 Nov. 1899 (BO, K, L); *Lörzing 716*, C, Tlerep, Prahu, N Sendara, 2000 m, buds, 24 Nov. 1912 (BO, L); *Steenis 5110*, W, Bogor, Tjiapuskloof, Gn. Salak, 800-1000 m, fl., 31 July 1932 (A, BO, K, L, SING); *Steenis 17615*, W, Bogor, Gn. Pangrango, 2500 m, st., 29 May 1950 (BO); *Winckel 1559*, W, Bogor, Tjadasmalang, nr. Tjidadap, S of Tjibeber, 1000 m, fl., fr., 11 Aug. 1923 (BO, K, L, SING).—Borneo: Sabah: *Aban Gibot SAN 60723*, Distr. Ranau, Kamp. Kilimu Ranau, 2.5 miles E of Ranau along Poring Rd, 2000 ft., fr., 18 Sep. 1967 (BISH, SAN); *Aban Gibot SAN 62024*, Distr. Tuaran, Kampong Parad, fr., 18 May 1968 (L, SAN, SAR); *Aban Gibot SAN 66831*, Distr. Ranau, Copper Mining Area, Mamut, buds, 2 May 1970 (L, SAN); *Aban Gibot SAN 95210*, Distr. Beluran, Bt. Monkobo, 1950 m, st., 15 Mar. 1982 (SAN); *Alabazo SH (SAN) A 3626*, Forest Distr. Jambunah, Kg Zanateir, 2500 ft., fr., 26 Mar. 1952 (L, SING); *Carr SF 27228*, Mt. Kinabalu, nr. Bundu Tuhan, 4000 ft., fl., 3 May 1933 (SING); *Chew & Corner RSBN 4398*, Mt. Kinabalu, Bembangan R., 5400 ft., st., 20 Feb. 1964 (K, L, SAN); *Clemens & Clemens 50693*, Mt. Kinabalu, Gurulau Spur, 5500 ft., fr., 4 Dec. 1933 (A, BM); *Clemens & Clemens 51173*, Mt. Kinabalu, Penibukan ridge, 4000 ft., fl., 6 Nov. 1933 (A, BM, K); *Cockburn SAN 84928*, Distr. Lahad Datu, Summit trail of Gn. Tribulation, Sg. Segama, 900 m, fr., 18 Aug. 1976 (K, L, SAN, SAR); *Madani SAN 89394*, Distr. Ranau, foot Bt. Ampuan, 2500 ft., fl., 18 Nov. 1978 (L, SAN, SAR); *Meijer SAN 51588*, Distr. Sandakan, Mt. Melian nr. Kiabu Labuk, 2800 ft., juv., 14 May 1965 (SAN); *Mikil SAN 31867*, Distr. Tambunan, Trusmadi above Kionop, juv., 10 Oct. 1962 (KEP); *Mikil SAN 37765*, Distr. Penampang, Suran Trail, 890 ft., fr., 15 Dec. 1963 (L, SAN, SAR); *Sarie SAN 28510*, Distt. Ranau, spur of Kg Tamis Tenompaok F.R., 4700 ft., yfr., 19 Feb. 1962 (K, KEP, L, SAN, SAR); *Sundaling SAN 129697*, Distr. Lahad Datu, FR Malau, fl., 30 July 1990 (SAN).—Brunei: *Ashton BRUN 1044*, Bt. Pagon ridge, 4750 ft., fr., Mar. 1958 (K, L, SAR). — Sarawak: *Ashton S 21116*, Bt. Lumut, Carapa Amau, Ulu Mujong, Hose Mts., 950 m, st., 14 Apr. 1964 (K, SAR); *Chai S 18535*, Gn. Matang, 800 m, fl., 31 July 1963 (A, K, KEP, L, SAN, SAR); *Chai S 35503*, Perupayang nr. foot of Apo Duat Range, Kelabit Highlands, Baram Distr., 4th Div., 1180 m, yfr., 14 Nov. 1974 (A, K, L, SAN); *Dyg. Awa & Lee S 51142*, Tama Abu Range, Bario, 4th Div., 1750 m, fl., 19 May 1988 (K, KEP, L, SAR); *Ilias Paie S 26012*, Ulu Ugong, Lawas, 2800 ft., fr., 19 Sep. 1967 (K, L, SAN, SAR); *Lee S 52496*, Bt. Tebunan, Ulu Trusan, Lawas,

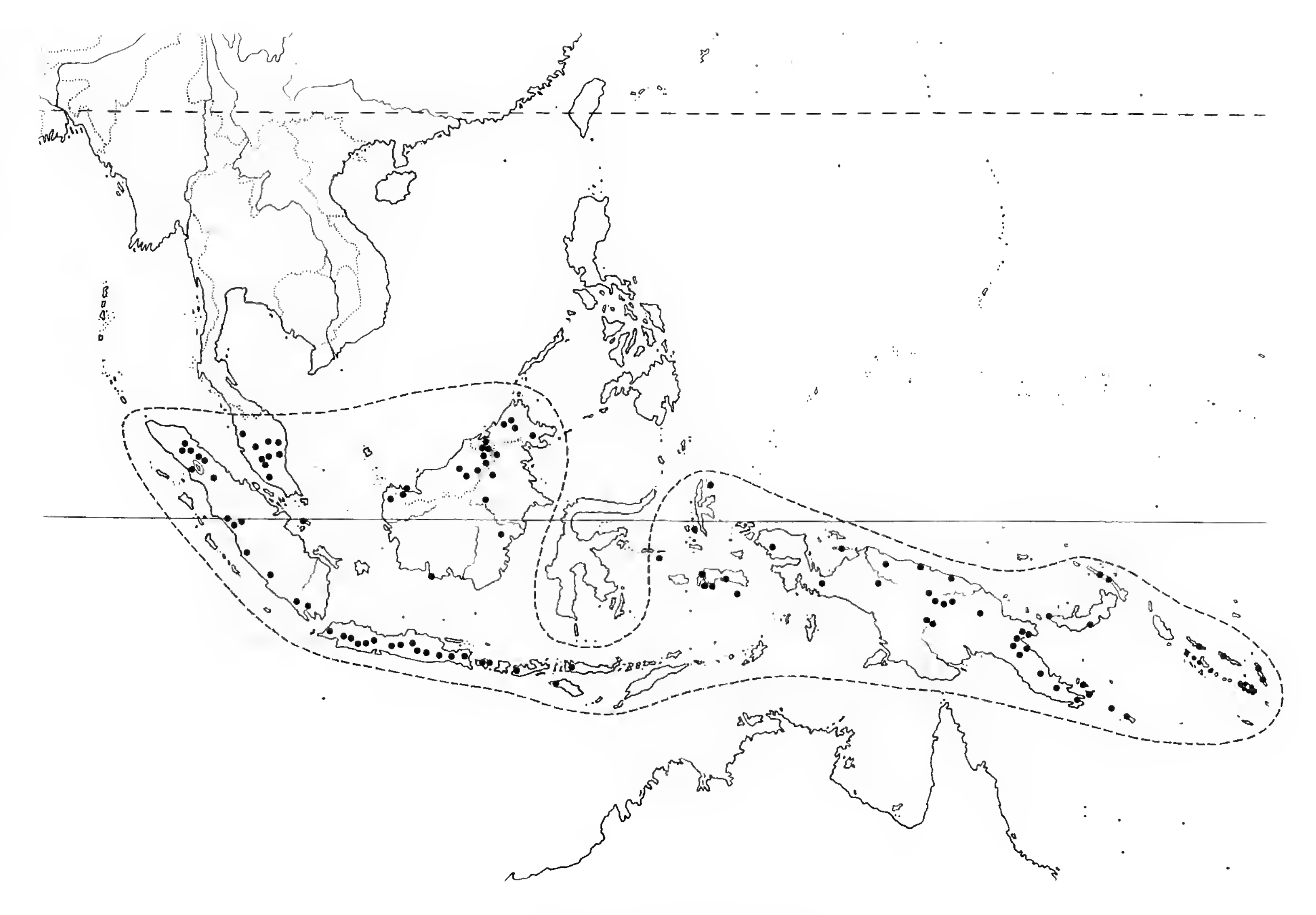


Fig. 8.—Distribution of ***Weinmannia fraxinea***.

5th Div., 1450 m, fl., 9 May 1986 (K, L, SAN, SAR); *Martin S 37053*, Gn. Mulu National Park, Tutoh, Baram, 4th Div., 1310 m, fl., 24 Feb. 1976 (K, L, SAN, SAR); *Murthy & Ashton S 22621*, Usun Apau, Long Nyalau, Dapoi, Tinjar, 700 m, st., 4 Apr. 1965 (A, K, L, SAN, SAR); *Nooteboom & Chai 1696*, Kalabit Highlands, Bario, daka sina kaja hill, 1000 m, yfr., 25 Mar. 1970 (BISH, K, KEP, L, SAR); *Pickles S 3777*, Mt. Kalulong, 3°14'N-114°41'E, 4310 ft., fr., 19 Feb. 1956 (BM, SAR).—KALIMANTAN: *Endert 3136*, W Kutei, L. Petak, 600 m, fl., 10 Sep. 1925 (BO, L); *Geesink 8953*, Kalimantan Timur, between Long Bawan and Panado, 3°52'N-115°42'E, 1000 m, fl., 7 July 1981 (L); *Jong bb 9670*, West Borneo, Ond. afd. Bengkajang, top Gn. Bawang, 1400 m, juv., st., 25 Mar. 1926 (BO); *Kostermans 7540*, Peak of Balikpapan, Gn. Beratus, 1200 m, st., 15 July 1952 (BO, K, L); *Kostermans 12903*, W. Kutei, Mt. Palimasan nr. Tabang on R. Belajan, 700 m, fr., 11 Sep. 1956 (BM, K, KEP, L); *Valkenburg & Storkdale 1082*, Kayan Mentarang Reserve, 2°51'N-115°55'E, 950 m, fl., 26 Nov. 1991 (A); *Yaeger 203*, Tanjung Puting, Kalimantan Tengah, 0 m, st., 16 Nov. 1985 (A).—LESSER SUNDA ISLANDS: ***Bali***: *Kostermans et al. KK&SS 162*, Bedugul forest region, Mt. Batukan complex, 1300 m, fl., 25 June 1958 (A, BM, BO, K, L, P); *Meijer 10400*, Mt. Agung, 8°20'S-115°30'E, st., 17 June 1976 (L); *Seuff 17, bb 17276*, Kluenkung, nr. Pengedjaran, 1200 m, fr., 22 Feb. 1933 (A, BO); *Steenis 8043*, Gn. Abang, 1500-2000 m, st., 9 Apr. 1936, (BO). ***Sumbawa***: *Kostermans 18439*, W Sumbawa, Mt. Batulanteh, Brangbossang, trail from Batudulang to Pusu, 800-900 m, st., 24 Apr. 1961 (K, L). ***Sumba***: *Verheijen 4028*, s.loc., buds (L); *Voogd 1901*, W Sumba, 500 m, fl., 30 Nov. 1934 (BO, L). ***Flores***: *Hoogland 12646*, W Flores, Poco Raneka nr. Ruteng, 1400 m, fl., 25 June 1975 (CANB, L); *Kostermans 22091*, W Flores, SE part Mbengen, 600 m, buds, 10 May 1965 (K, L); *Schmutz 4588*, Nunang, 1100 m, fr., 2 Feb. 1980 (L); *Verheijen 4360*, Karat-Lelak, st., 16 July 1974 (L).—MOLUCCAS: ***Morotai***: *Kostermans 1097*, Gn. Pare 2, 900 m, 26 May 1949, (BO, L). ***Bacan***: *Haan 2, bb 23122*, nr. Masurung, 500 m, st., 12 Aug. 1937 (A, BO, L). ***Sula Isls.***: *Atjeh* (*Exp. v. Hulstijn*) *383*, Eil. Sulabesi (= Sanana), Gn. Patahoi, fl., 1913-14 (BO, L). ***Seram***: *Burley et al. 4363*, 40 km E of Masohi in Wae Rutan/Wae Ruwata (Ruwa) catchment areas, 150 m, fl., 7 Dec. 1990 (A, K, KEP, L, P); *Rutten 1649*, W Ceram, W of Piru, 0-100 m, fl., 25 Sep. 1918 (BO, K, L); *Rutten 2221*, C Seram, H Elate S of Railiu, 400 m, fl., 13 May 1919 (BO, L). ***Ambon***: *Burlage 253*, Gn. Tuna, fl., 17 July 1900 (BO); *Dumont d'Urville 131?*, s.loc., fl., Oct. 1823 (P); *Kornassi 1181*, Gn. Hatumesen, 0-100 m, fl., 25 Apr. 1918 (BO, K, L); *Kuswata & Soepadmo 250*, Waai, slope of Mt. Salhutu, 100-200 m, fr., 7 July 1959 (A, BISH, BM, K, KEP, L, P); *Matatula 5, bb 14261*, nr. Puta, kamp. Hatu, 250 m, st., 14 Dec. 1929 (BO); *Rant 112*, Karang panjang, behind Soja rd., fr., 30 May 1929 (BO); *Vriese & Teysmann s.n.*, s.loc., fl., 1859-1860 (L); *Wiljes-Hissink 21*, foothills of Salahutu Mt. nr. Wae, 200 m, buds, Apr. 1948 (A); *Zippel 72d*, s.loc., fr., Sep. 1828 (L). ***Uli Asser Isls.***: *Malessij 4, bb 14303*, Haruku, nr. Taëhenitu, 300 m, fl., 20 Mar. 1930 (BO). ***Banda***: s.coll., *s.n.*, s.loc., fl. (L). ***Cult. in Hort. Bog. ex Moluccas***: *Forman 51*, J130, fr., 25 Feb. 1956 (A, BO, K, L); *Jacobs s.n.*, J130a, male fl., 12 Mar. 1958 (BM, K, L, P).

LOCAL NAMES.—SUMATRA: Antahasi or Atahasi (Batak language, Toba), Boentoba (Toba), Resak kero (Malay language), Boenga Loetih (Lampung lang.), Bringin tandoek (language?).—MAL. PEN.: Kasai bukit (*Burkill & Holttum SF 6853*), Sentang (*Whitmore FRI 3881*), Pa'ang (*Bidin CF 4200*).—JAVA: ***Sundanese***: Ki merak(h), Karo tjok, Ki papatong, Kihiris, Kiringit, Tjirome, Tjeremeh, Ki Tjereme, Ki mèong, Angtiet passang, Kibiroe, Ki adjag, Ki-papattong. ***Javanense***: Dali kling or Dalikeling, Wlingi, Kelis, Pantjalkidang, Sampar kedang, Gagar, Kerjemé, Serak, Lere, Gringging, Damaran, ?Klis, ?djeng gitri, Nagasari gunung, Sap(i)enan, Sadan, Tembajang or Tèmbagan, S(e)riwalik, Wutu kunjet. ***Language not specified***: Damaran (*Backer 16223*), Ki soeren goenoeng (*Koorders 26546*), Legarie Tjantigi (*Kalshoven VI*), Pasang kengkeng (*Voogd 721*), Kajoe djaran (*Winckel 1963*).—BORNEO: Tekaran(u) (Kelabit), Uban (Iban), Tansang Lang (Iban), tkaran (*Nooteboom & Chai 1696*), Kayu-papan (Murut).—LESSER SUNDA ISLANDS: Kémérak(h)an (Balineese lang.), Larang (Flores).—MOLUCCAS: Marah, k = Doka2ra = Sela, k (Tobela lang., Bacan), Daon mejang (Ambon), Kahoenar (Malay lang., Ambon), Lagoendi hoetan (Malay, Ambon dialect), Taheroe (Malay, Ambon dialect), Meongmerah (Malay, Ambon dialect), Moöetoea (Haruku lang.).

LOCAL USES.—BORNEO: The leaves are used for dying cloth; they are boiled in water and then mixed with clay to make a blackish dye (*Chai S 35503*). Firewood.

NOMENCLATURE AND TYPIFICATION.—HOOGLAND worked extensively on the nomenclature and typification of *Weinmannia fraxinea* and its synonyms. Several lectotypes that he had chosen are formally designated here.

Under article 42.1 of the International Code of Botanical Nomenclature (GREUTER 1994), *Pterophylla fraxinea* D. Don, the basionym for *Weinmannia fraxinea*, was validly published in 1830 (*descriptio generico-specifica)* and should not be considered a *nomen nudum*.

For the names published by SCHLECHTER and placed in synonomy here, as well as for *W. borneensis* Engl., and for *W. pullei* Schltr. and *W. virgulata* Schltr. (see HOPKINS 1998b), the holotypes at Berlin have not been destroyed (see BERNARDI 1964).

TAXONOMY AND VARIATION.—As circumscribed here, *Weinmannia fraxinea* is a widespread species that shows a complex pattern of variation in the number, size, shape and texture of the leaflets and in the indumentum. *Weinmannia blumei*, the name usually applied to this species in western Malesia, is placed in synonomy with *W. fraxinea* here for the first time, as are several names from Borneo and New Guinea that were regarded by BERNARDI (1964) as distinct. The variation in *W. fraxinea* cannot be consistently divided into discrete units either morphologically or geographically, i.e. it shows "checkerboard" variation, and can thus be regarded as an ochlospecies (CRONK, in press; WHITE 1962). Since the variants grade into one another, division into infraspecific taxa is unwarranted. However, it is sometimes useful to be able to name variants, especially at a local level, and in this case I suggest following the example of HUXLEY & JEBB (1993) who propose the use of informal nicknames for the most distinctive variants of ochlospecies (e.g. "*dulitensis*" for the large, rubbery leafleted form; "*blumei*" for specimens with medium-sized, chartaceous leaves, etc.). However, there are too many intermediate collections for nicknames to be applied consistently to all the material in *W. fraxinea*.

The majority of collections from throughout the range have medium-sized, chartaceous to subcoriaceous leaflets, medium-sized and usually caducous stipules, and the indumentum on the axes varies from puberulent to tomentose (Fig. 7A). The flower buds are usually pinkish and the flowers whitish. In Sumatra, the Malay Peninsula, Java and New Guinea, some collections have smaller leaflets (Fig. 7D) (e.g. *Koorders 7646*, Java; *Steenis 3617*, *Rappard S27*, Sumatra; *Cockburn FRI 11030*, Malay Peninsula; *Stevens LAE 58123*, *Woods 2718*, New Guinea), the largest lateral leaflet per leaf exceptionally as small as 2.2 × 0.9 cm. These small-leafleted variants usually occur at high altitude though specimens with medium-sized leaflets sometimes occur at similar elevation. The inflorescences tend to be short and less well developed than in material from lower elevation (i.e. fewer partial inflorescences; dyads not tetrads) and the flowers are usually white.

Other collections from these four areas and from Borneo have exceptionally large leaflets, up to 12 × 3.5 cm. The leaflets vary in texture from chartaceous to coriaceous, but when coriaceous, they often have minutely prominent or contrastingly coloured venation and a dense reticulum of tertiary and quaternary veins. In these specimens, the axes are glabrous or subglabrous and the stipules are larger and more persistent. In the Malay Peninsula material like this has been named *W. blumei* var. *major* (e.g. *Ridley 16029*, *Wray & Robinson 5319*); in Borneo, *W. dulitensis* (e.g. *Clemens 51173*, *Hopkins & Bradford 5013*); and in New Guinea, *W. alta* (e.g. *Smith NGF 1355*, *Lam 1574*). In Sumatra, collections include *de Wilde & de Wilde-Duyfjes 14151* from Gn. Leuser, Aceh Province. However, the shape of the lateral leaflets is not always the same, and varies from lanceolate or elliptical and ± cuneate at the base, to ovate with the base rounded and conduplicate (Fig. 7B). In vivo, young stems and leaves are rubbery and difficult to press (HOPKINS & BRADFORD pers. obs.). In *W. fraxinea* "*dulitensis*" from Borneo, the inflorescence axes are reddish, the racemes long and robust, the flower buds pink or bright red and the flowers pinkish at anthesis (Fig. 2C,D).

Some other collections from Borneo have ovate lateral leaflets that are medium-sized, subcoriaceous, and the base is rounded on one or both sides but not conduplicate (Fig. 7C). They sometimes dry black and can be densely hirsute along the abaxial surface of the midrib. They correspond to *W. borneensis* (e.g. *Ampon et al. SAN 71837*, *Aban Gibot SAN 56354*, *J. & M.S. Clemens 32641*).

In Flores and Seram, the leaflet margins are rather distinctly crenate (e.g. *Hoogland 12646*, *Schmutz 30621*). Some specimens from the islands of Milne Bay Province, Papua New Guinea have leaflets with strongly acroscopic crenations (e.g. *Brass 27428* and *Gideon LAE 57278*,

both from Misima Island) but the leaflets here are larger than in the Lesser Sunda Islands.

In the Moluccas, the leaflets are typically elliptical or lanceolate and the base of lateral leaflets, especially the most distal pair, is strongly unequal, being attenuate on one side and concave on the other (Fig. 7E) (e.g. *Kornassi 1181*, *Kuswata & Soepadmo 250*, *Malessij bb 14281*, *Teysmann s.n.*, Ambon; *Rutten 2221*, Seram). A few collections from the Cycloop Mts., Irian Jaya are rather similar (e.g. *Koster BW 4302*). In both the Moluccas and New Guinea some collections are glaucous on the underside of the leaflets (e.g. type of *W. hypoglauca* from Irian Jaya; *de Wiljes-Hissink 21*, Ambon).

Weinmannia fraxinea is less variable than some other ochlospecies, such as *Myrmecodia tuberosa* Jack in which 16 informal entities were recognised (HUXLEY & JEBB 1993), but nevertheless it shows many of the traits listed by CRONK (in press) as characteristic of this type of complex species. It has strongly polymorphic, non-hierarchical variation where the characters vary independently of one another and largely independently of geography and ecology. It has a widespread distribution and shows considerable ecological plasticity, occurring for instance in New Guinea from near sea level to over 2000 m on a variety of soil types. While distinct variants can sometimes be recognised at a local level, they intergrade when the whole range of the species is considered. Similar morphologies are often found in widely separated localities and sometimes appear to be polytopic, while other variants occur in only one region. In some cases, at a particular locality, there can be two distinct variants present which do not intergrade, although in another locality they do. In common with many ochlospecies, *W. fraxinea* belongs to a large genus and has closely related, monomorphic satellites, such as *W. devogelii* H.C. Hopkins in Sulawesi and *W. macgillivrayi* Seem. in Vanuatu.

Although variation is not due to interspecific hybridization, nor does *Weinmannia fraxinea* appear to be a series of apomictic microspecies (see CRONK, in press), the morphology of flowers on herbarium specimens suggests a complex and variable breeding system (Table 1). Clearly field observations are needed but current evidence indicates that *W. fraxinea* is predominantly dioecious or polygamodioecious in some regions and hermaphroditic in others. Successive cycles of flowers of different sexes on one plant, as seen in certain Sapindaceae (VAN WELZEN 1990) and which may occur in some of the Pacific species of *Weinmannia*, would not produce the pattern that has been observed in this species to date. For instance, herbarium specimens from plants in cultivation at the Botanical Garden at Bogor, which originated in the Moluccas where *W. fraxinea* is morphologically dioecious, are unisexual and provide no evidence that the trees change sex. It seems likely that variation in the breeding system contributes to taxonomic complexity and it is possible that some populations are apomictic. The fact that distinct variants sometimes do not intergrade where they occur together suggests a complex breeding system and at least partial barriers to gene flow.

CRONK (in press) discusses two hypotheses for the origin of ochlospecies. The Prance hypothesis proposes that this type of polymorphic variation could have arisen in allopatric populations separated from one another in refugia during dry periods of the Pleistocene. The geographical region where *W. fraxinea* has its present distribution was certainly subject to considerable fluctuations in climate and sea level during this period. In a second hypothesis, CRONK (in press) proposes that the rapid expansion of a colonising species with wide ecological tolerance could give rise to the geographically unstructured variation seen in ochlospecies. With time and outcrossing, this variation would become ecogeographically sorted and one or more less-variable species could emerge. This hypothesis seems particularly apt for *W. fraxinea* which has wide ecological tolerance and is often a pioneer. As suggested by CRONK, molecular techniques could be used to investigate the genetic structure and origin of ochlospecies.

2. **Weinmannia clemensiae** Steenis

J. Bot. 72: 3 (1934); Bernardi, Bot. Jahrb. Syst. 83: 166, t. 18 (1964); Cockburn, in Kinabalu Summit of Borneo, chapter 7: 185, fig. only (1978).—Type: *J. &*

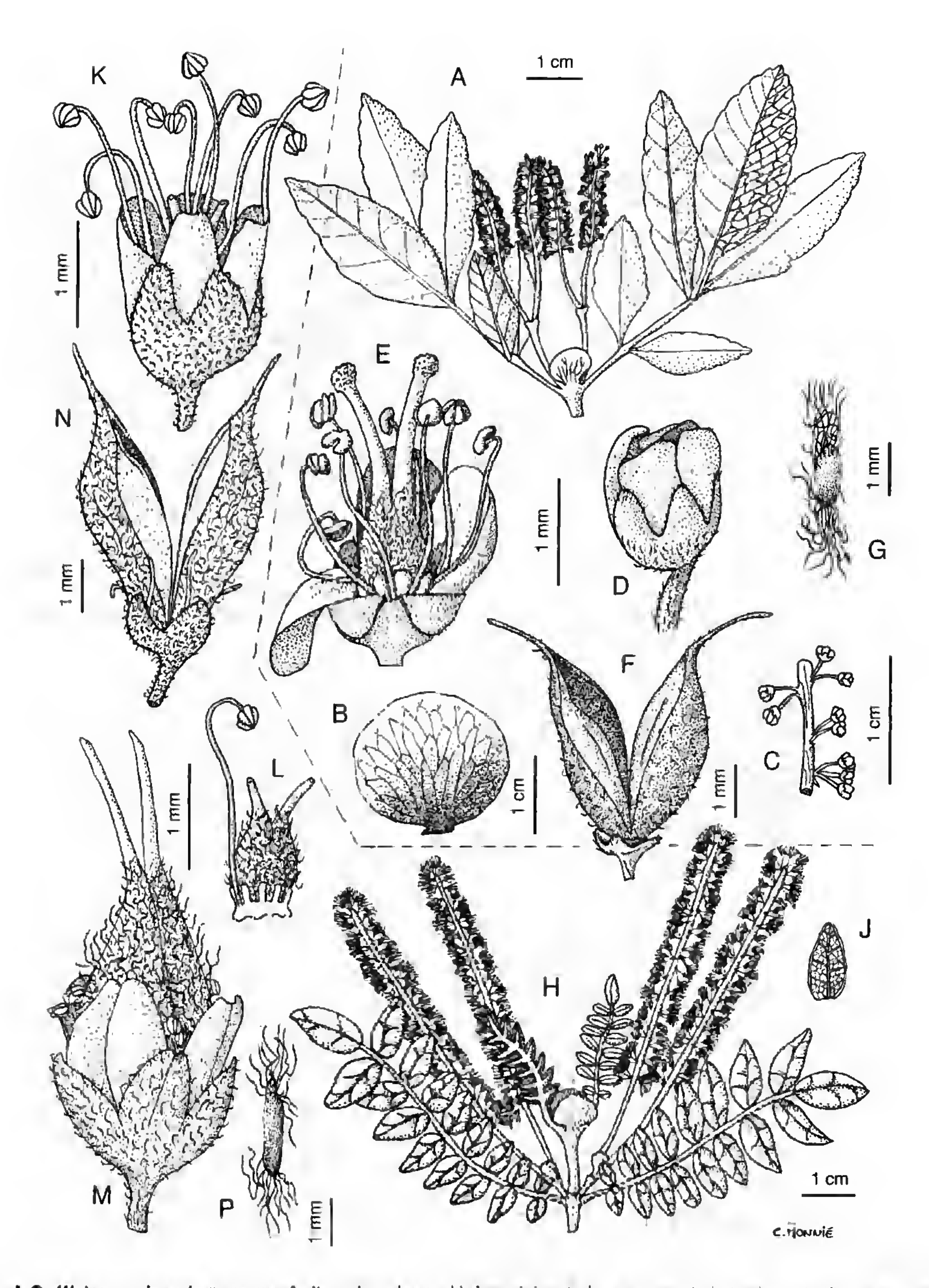


Fig. 9.—**A-G**, ***Weinmannia aphanoneura***: **A**, flowering shoot with imparipinnate leaves, rounded stipule and inflorescence of two dyads; **B**, stipule; **C**, section of rachis of raceme showing flowers inserted in fascicles, the floral bracts already fallen; **D**, flower bud; **E**, female flower with one petal removed; **F**, dehisced capsule; **G**, seed. (A, *Chew Wee-Lek 380;* B, E, *Clemens 33076;* C, D, *Paie S26531;* F, G, *Endert 4125*).—**H-P**, ***Weinmannia clemensiae***: **H**, flowering shoot with imparipinnate leaves and an inflorescence of two dyads, the apical bud continuing to grow and producing a pair of young leaves; **J**, abaxial surface of a lateral leaflet; **K**, flower, probably male; **L**, detail of K with perianth removed to show gynoecium, disc lobes and a single stamen; **M**, female flower, note short filaments; **N**, dehisced capsule; **P**, seed. (H-L, *Beaman 9132*; M, *Chew & Corner RSNB 4508*; N, P, *Clemens 50877*).—Drawn by C. MONNIÉ.

M.S. Clemens 27880 (Sabah), Mt. Kinabalu, in low jungle near Kamborangah, 2400 m, 7 Jan. 1932 (holo-, BO!; iso-, K! [photo at KEP], L!).

Treelet or tree, 1.5-10 m high. Young stems and leaf rachises densely tomentose-velutinous, older stems tomentose becoming ± glabrous with numerous lenticels; stems terete, relatively thick, 3-5 mm diameter, nodes somewhat thickened and leaf scars prominent. Internodes often short, 0.5-1.7 cm. Branching not dichotomous. Stipules usually caducous, ± orbicular, up to 1 × 1.2 cm, base narrowing, apex broadly rounded, abaxial surface densely sericeous especially towards the base, adaxial surface shortly velutinous. Leaves imparipinnate, with 6-13 pairs of lateral leaflets, total length up to 13 cm including petiole 0.5-1 cm long; rachis segments 0.4-0.9 cm long; petiole and rachis segments terete, densely tomentose-velutinous, diverging from the stem at an angle of almost 90° especially at growing tips; leaflets bullate and carinate, the margins strongly recurved and often rolled; lateral leaflets oblong or somewhat ovate, the largest per leaf 1.4-2.7 × 0.6-1 cm, leaflets towards the base smaller, inserted ± at 90° to leaf rachis, base equal, rounded to cordate, apex broadly acute; terminal leaflet elliptical, 1.9-3.3 × 0.7-1 cm including petiolule of 0.3-0.5 cm, blade scarcely larger than largest lateral leaflets, apex acute; blades coriaceous, the upper surface puberulent or glabrous when the cuticle thick, sparsely to densely pubescent below, the midrib sericeous; sometimes punctate (bases of hairs); margin crenate but crenations usually obscured, 5-7 notches on each side in the lateral leaflets; on upper surface midrib indented, secondary veins ± at 90° to main vein, tertiary venation obscure; midrib prominent below.

Inflorescence a pair of opposite, lateral dyads, the apical bud of the main stem between the peduncles of the dyads densely sericeous, often continuing to grow vegetatively during flowering; bud at apex of peduncle in angle between the racemes sericeous; sometimes a few successive nodes on one shoot producing dyads simultaneously; peduncles 0.3-0.7 cm long; racemes up to 10.5 cm long; peduncles and axes of racemes densely tomentose-velutinous; inflorescences and infructescences dense. Floral buds inserted in fascicles, floral bracts obovate-carinate, with short flattened hairs, up to 1-1.5 mm long, caducous. Flowers unisexual (or sometimes bisexual?); pedicel 1-1.5 mm long, with short erect hairs; calyx lobes 0.8-0.9 × 0.6-0.8 mm, hirsute; petals obovate or almost circular, 1.1-1.5 × 1-1.1 mm, rounded at apex, margin ciliolate; disc lobes 0.4-0.5 mm long, oblong or broadly oblong; in male flowers: filaments ca. 2.5 mm long, ovary ca. 0.6 mm, densely pubescent, styles 0.1 mm, incurved (some flowers in same inflorescence have ovary 0.9 mm long and styles 0.8 mm long, straight, and may be bisexual); in female flowers: filaments up to 1.9 mm long, ovary 1.5-2 mm long, densely pubescent, styles ca. 1 mm long, straight, pubescent at base.

Capsules up to 3.7-4.5 × 1.8-2.2 mm at dehiscence, plus styles up to 1.5 mm long, the exocarp densely pubescent; calyx lobes persistent; central column weakly developed. Seeds immature, ca. 0.9 mm long, comose at both ends.—Fig. 2B, 9H-P, 10.

Juvenile foliage.—Seedling leaves: blade thin, chartaceous, margin strongly toothed and flat, not recurved; lateral leaflets few (ca. 4 pairs), mid green or reddish; stipules sometimes toothed (*Hopkins & Bradford 5015*). Saplings and coppice shoots: blade coriaceous, lateral leaflets up to 18 pairs, of similar size to those of adult foliage but scarcely recurved; venation indented above; margin distinctly toothed (*Hopkins & Bradford 5016*).

Breeding system.—Dioecious or polygamodioecious? Few collections have flowers at anthesis. Specimens with immature fruits have short filaments, suggesting they have developed from functionally female flowers.

Field characters.—Adult foliage darkish green above, paler below with main vein brown or pink; leaf rachises and stems brown; stipules satiny mid green and paler than foliage. Buds green, white or brown from indumentum; new growth densely velutinous and sometimes reddish. Flowers pinkish brown or deep cream-pink; calyx blood red; corolla pink or pink-white; stamens cream; whole inflorescence pink and downy. Immature fruits pink with red styles, infructescence axis tinged pink.

Distribution and ecology.—Endemic to Mt. Kinabalu and Mt. Tambuyukon in Sabah. Restricted to stunted forest on strongly ultramafic soil at (1640-)1900-2600 m. Habitats described as low mossy and xerophyllous scrub forest, open ridges, oak-laurel forest, and forest dominated by *Leptospermum* and *Dacrydium*. Other associates include *Nepenthes rajah*. Probably all populations occur within the boundary of Kinabalu Park, whose protection is therefore crucial to the continued survival of this species.

Material examined.—**Borneo: Sabah:** *Barkman & Buin 141*, Layang Layang, 2600 m, fl., 1 Mar. 1995 (*KIN); *Beaman 9132*, Ranau District, East Mesilau River, nr. Mesilau Cave, 6°03'N-116°36'E, 1950-2100 m, fl., 26 Mar. 1984 (K, L); *Beaman 9837*, Ranau District, Pig Hill on E side of Mt. Kinabalu, 6°03'N-116°36'E, 2000-2300 m, st., 25 May 1984 (A, K, L); *Chew & Corner RSBN 4364*, Mt. Kinabalu, Pig Hill, 7000 ft., fl., 18 Feb. 1964 (K, L, SAN); *Chew & Corner RSNB 4508*, ibid., yfr., 24 Feb. 1964 (A, K, L, SAN); *Chew & Corner RSNB 4755*, Mt. Kinabalu, Mesilau Cave, 6000 ft., st., 29 Mar. 1964 (K, L, SAN); *J. & M.S. Clemens 50793*, Mt. Kinabalu, Gurulau spur, 7000-9000 ft., fl., 6 Dec. 1933 (A, BM, K, L); *J. & M.S. Clemens 50877*, ibid., 8000 ft., fr., 8 Dec. 1933 (A, BM, K, L); *Hopkins & Bradford 5011*, Mt. Kinabalu, Pig Hill, 116°38'E-6°03'N, 2250 m, yfr., 5 Mar. 1996 (KIN, P, MO); *Meijer SAN 28737*, Ranau District, Mt. Tambuyokan, 6000-7000 ft., st., July 1961 (K, L, SAN); *Meijer SAN 34617*, ibid., 6000 ft., st., July 1961 (SAN); *Meijer SAN 48098*, Mt. Kinabalu, Ranau District, opp. Kinabalu cave, Kinabalu Nat. Park, 8000 ft., st., 20 Feb. 1965 (K, L, SAN); *Mikil SAN 47041*, Ranau Dist. Kinabalu Park, Mesilau base camp, 5000 ft., st., June 1964 (SAN); *Nais et al. SNP 3675*, Kinabalu Park, Mt. Tambuyukon, 8000 ft., fl., 16 Mar. 1991 (KIN); *Nais et al. SNP 4896*, ibid., between camp III and summit, fl., 6 Oct. 1990 (KIN); *Philips SNP 2318*, Mesilau landslide, fl., 28 May 1986 (KIN); *Whitehead s.n.*, Kinabalu, 9000 ft., st., Mar. 1888 (BM).

(*KIN refers to the herbarium at Kinabalu Park HQ).

As noted in the type description, this species appears to be most closely related to *W. urdanetensis* from the Philippines and the Highlands of New Guinea. In both species there are numerous, small leaflets arranged at right-angles to the leaf rachis and the secondary veins are at right-angles to the midrib. *Weinmannia clemenisae* has characteristically bullate leaflets with the margins recurved so that they can not be flattened. There is a slight tendency to bullate leaflets in *W. urdanetensis* but it is not nearly so pronounced. In both species the upper cuticle is sometimes thickened and the structure of the inflorescence is similar. The seeds of *W. clemensiae* are comose at each end, not hairy throughout as in *W. urdanetensis*.

3. **Weinmannia aphanoneura** Airy Shaw

Bull. Misc. Inform. 1940: 260 (1940); Bernardi, Bot. Jahrb. Syst. 83: 160 (1964).—Type: *P.W. Richards 1716* (not 6716 as given in protologue), Sarawak, Dulit Ridge, open moss forest, ca. 1400 m, 11 Sep. 1932 (holo-, K!, photo at KEP).

Shrub or tree 2-20 m high and up to 35 cm dbh. Young woody stems ± glabrous or adpressed puberulent, soon glabrescent, older ones glabrous with numerous lenticels, nodes sometimes ± thickened and leaf scars prominent; branching not usually dichotomous. Stipules often persistent at distal nodes, suborbicular and usually flat, not recurved, up to 1.7 × 1.9 cm (rarely spathulate, ca. 0.6 × 0.4), base constricted, apex broadly rounded, abaxial surface glabrous or shortly strigose especially towards the base, adaxial surface glabrous. Leaves imparipinnate, with (0-)1-4 (-5) pairs of lateral leaflets, total length up to 16 cm, including petiole of 0.7-2.8 cm; rachis segments 0.5-1.9 cm long; petiole and rachis semiterete, adaxial side flattened, slightly ridged or channelled, sometimes narrowly winged, especially towards the point of insertion of the leaflets, wings extending outwards up to 1 mm on either side of mid line, petiole and rachis glabrous or tomentose either on adaxial or abaxial surface but not both, usually inserted at an acute acroscopic angle; lateral leaflets narrowly elliptical or narrowly obovate, the largest 2.4-7 × 0.6-1.9 cm, the base unequal, ± sessile, cuneate, apex acute to obtuse; apical leaflet narrowly elliptical, narrowly obovate to obovate, scarcely larger than the largest lateral leaflets, 3-9.4 × 0.7-2.7 cm including the narrowly cuneate to attenuate base 0.3-1.2 cm long, apex acute to obtuse; blades coriaceous, glabrous and sometimes shiny above, glabrous below, characteristically drying grey or

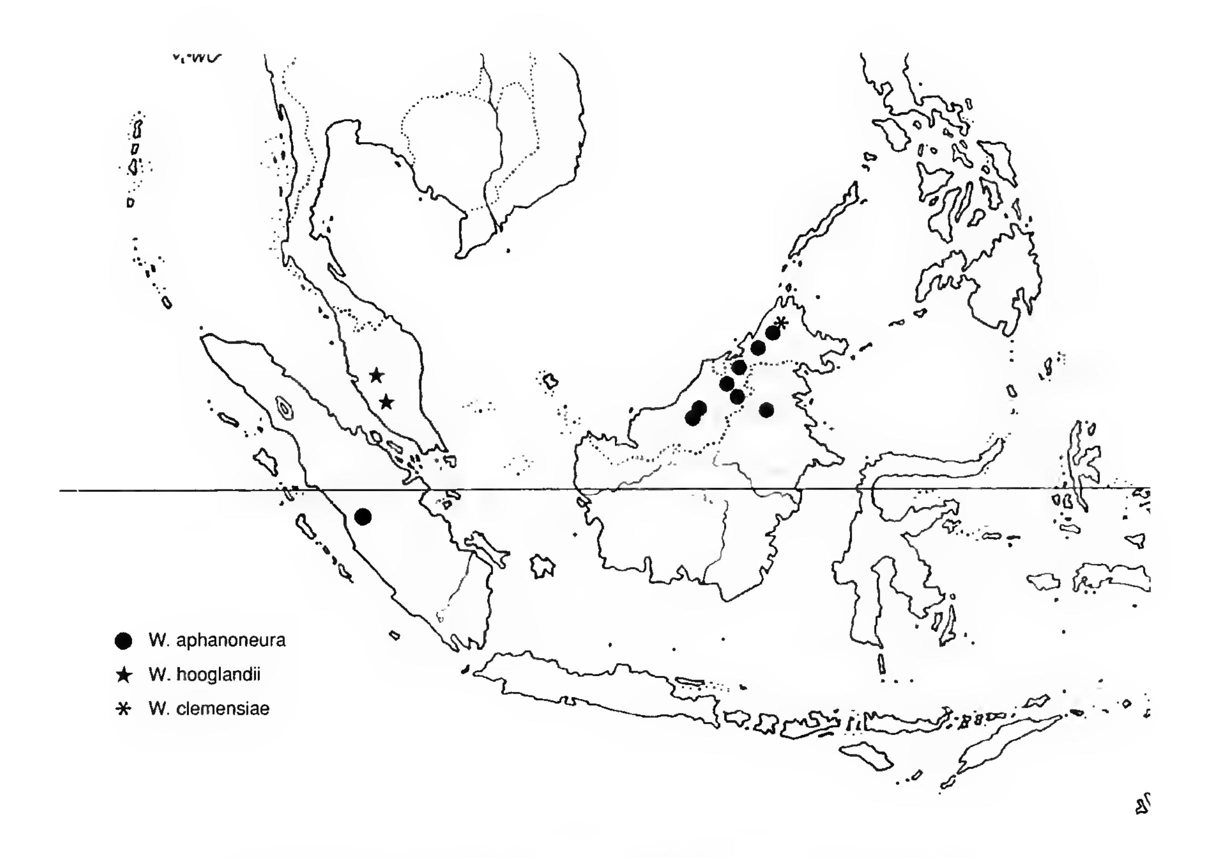


Fig. 10.—Distribution of ***Weinmannia aphanoneura, W. clemensiae*** and ***W. hooglandii***.

dark chestnut above and chestnut below; not punctate; margin crenate, 6-11 notches on each side of the largest lateral leaflets; midrib slightly depressed above, prominent below and sometimes pubescent to tomentose at base, secondary and tertiary venation ± flat on both surfaces or often obscured especially on the upper surface by the thick cuticle; reticulum not dense.

Inflorescence 1 or 2 pairs of opposite dyads, the apical bud of the main stem between the central dyads shortly sericeous, rarely continuing to grow vegetatively during flowering; bud at apex of peduncle in angle between racemes shortly sericeous; sometimes dyads produced in axils of leaves at subdistal nodes; peduncles ca. 0.3-1.9 cm long, racemes usually not longer than the leaves (7-8 cm) but sometimes up to 14 cm long; peduncles glabrous or adpressed puberulent, axes of racemes puberulent, rarely tomentose; stipules at node at top of peduncle sometimes persistent and either free and orbicular or connate at base to form a cup-shaped structure. Floral buds inserted in fascicles; floral bracts carinate, ca. 1.6 mm long, margin with minute glandular teeth, shortly hairy on abaxial surface. Flowers unisexual; pedicel 1.8-3.6 mm long, puberulous; calyx lobes 0.5-0.8 × 0.4-0.9 mm, glabrous; corolla often rotate, petals oblong or irregularly obovate, 1.2-1.5 × 0.7-0.8 mm, rounded or emarginate at apex; disc lobes 0.3-0.5 mm long, oblong and discrete or with thin flanges on either side so that the 8 lobes form an almost continuous disc; in male flowers: filaments 2.1-2.6 mm long, ovary 0.5-0.7 mm long, pubescent, styles 0.1-0.2 mm long, incurved; in female flowers: filaments up to 1.7 mm long, ovary ca. 1 mm long, densely pubescent, styles ca. 1.8 mm long, straight, stigmas capitate, papillose.

Capsule 2.5-3.5 × 1.3-1.5 mm at dehiscence, the styles up to 1.5 mm long, the exocarp pubescent; calyx lobes persistent; central column sometimes present. Seeds ca. 0.9 mm long, comose at both ends, the hairs to 1.5 mm long.—Fig. 9A-G, 10.

BREEDING SYSTEM.—Dioecious.

FIELD CHARACTERS.—Bark scaly dark brown, outer bark reddish, inner bark brownish, sap wood pale yellow (*Pitty & Ogata SAN 63292*). Stem pink; petioles, midrib on underside of leaflets and inflorescence sometimes magenta. Buds red; flowers white to pink; calyx pink or red; corolla cream, pale pink or reddish; filaments white with pale pink anthers. Fruits crimson.

DISTRIBUTION AND ECOLOGY.—Montane forest in Borneo and Sumatra (one record), at 1175-2560 m. Habitats described as open moss forest, ridge top forest, submontane heath forest and ericaceous mossy forest. Locally common.

MATERIAL EXAMINED.—**SUMATRA:** *Nagamasu 3641*, West Sumatra, summit of Gn. Rasam, ca. 10 km S of Danau Diatas, 1°10-11'S-100°44-45'E, 2500-2565 m, fl., 18 Feb. 1989 (L).—**BORNEO: SABAH:** *Aban SAN 76507*, Mt. Kinabalu, Ranau District, above power station, st., 11 Mar. 1973 (SAN); *J. & M.S. Clemens 29476*, Mt. Kinabalu, Tenompok, 5000 ft., fl., 2 May 1932 (A, BM, K, L); *J. & M.S. Clemens 33076*, Mt. Kinabalu, Marai Parai, headwaters of Sadikan, 5000 ft., fl., yfr., 5 May 1933 (A, BM, K, L). **SARAWAK:** *Anderson 4507*, Baram District, Gn. Mulu, path from Melinau Paku, 4800 ft., buds, 30 June 1961 (A, K, L); *Brunig S 8785*, Bintulu District, Merurong plateau, Bt. Bandong, fl., 15 May 1960 (A, K, L); *Burtt & Martin 5487*, 4th Div., Gn. Murud, 3°55'N-115°31'E, 7800 ft., fl., 12 Oct. 1967 (SAR); *Chew Wee-Lek 380*, Baram District, Gn. Mulu, 4° 5'N-114°55'E, 5000 ft., buds, 16 June 1962 (A, K, L); *Chew Wee-Lek 388*, ibid., fl., 16 June 1962 (A, K, L); *Ilias Paie S 26481*, Gn. Murut, Ba Kelalan, Lawas, 7700 ft., fl., 10 Oct. 1967 (K, L); *Ilias Paie S 26531*, Gn. Murut, Ulu Pahdapar, Ba Kelalan, Lawas, 7750 ft., fl., 13 Oct. 1967 (K, L). **KALIMANTAN:** *Endert 4125*, Ond. Afd. W. Koetai, b/d Kemoel, 1500 m, fr., 14 Oct. 1925 (L).

***W.* cf. *aphananoneura*.**— **BORNEO: SABAH:** *Pitty & Ogata S 63292*, Tenom District, Gn. Anginon Sapong, 3900 ft., fl., 20 Nov. 1968 (A); *Ogata 11614*, ibid., 1175 m, 20 Nov. 1968 (L).

LOCAL NAME.—Maba (Iban).

4. Weinmannia hooglandii H.C. Hopkins & J.C. Bradford, **sp. nov.**

A W. fraxinea *foliolis lateralibus parvioribus (maximis < 2 cm longis, non > (2.8-) 3.5 cm longis) oblongis apice late acuto (non lanceolatis apice anguste acuto), venatione reticulata conferta, areolis parvioribus, inflorescentia unica pare dyatum lateralium (non 2 nec 3 paribus dyatum vel tetratum) diversa.*

TYPE.—*T.C. Whitmore FRI 12582*, Peninsular Malaysia, Pahang/Selangor, Gn. Ulu Kali, forested gully, 5600 ft., 9 Sep. 1969 (holo-, KEP!; iso-, A!, K!, L!, SAN!).

Shrub or small tree 1.2-5 m × 4 cm dbh. Young woody stems tomentose or velutinous, older ones glabrescent with numerous lenticels, branching not dichotomous. Stipules persistent or not at distal nodes, ± orbicular, up to 0.5 × 0.6 cm, base constricted, apex broadly rounded or flattened, abaxial surface shortly strigose especially towards the base, adaxial surface glabrous. Leaves imparipinnate, with 3-8 pairs of lateral leaflets, total length 5-7 cm long; petiole 0.8-1.5 cm long, rachis segments 0.4-0.8 cm long, petiole and rachis terete, slightly wider towards the point of insertion of the leaflets, often densely tomentose and especially so along adaxial side; lateral leaflets ± oblong to narrowly ovate, slightly imbricate the largest 1.6-2 × 0.5-0.6 cm, the most proximal leaflets smaller, ca. 0.7 × 0.4 cm, base unequal, sessile, cuneate, apex broadly acute; apical leaflet narrowly elliptical, scarcely larger than the largest lateral leaflets, 1.5-2.3 × 0.5-0.8 cm, base attenuate, apex acute; blades coriaceous, glabrous and sometimes shiny above, glabrous below, not punctate; margin crenate, ca. 3-7 notches on each side of the largest lateral leaflets, margin minutely revolute; midrib slightly depressed above, prominent below and sometimes shortly strigose especially towards the base, secondary and tertiary venation ± flat on both surfaces or often obscure on the upper surface, reticulum relatively dense and drying darker than the remainder of the blade.

Inflorescence a pair of lateral dyads, the apical bud of main stem between the peduncles shortly sericeous; bud at apex of peduncle between racemes shortly sericeous; peduncles ca. 0.4-0.5 cm long, strigose; racemes up to 6 cm long,

the axis pubescent or tomentose. Floral buds inserted in fascicles; floral bracts carinate, ca. 1 mm long, minutely hairy; pedicel 1.5-3 mm long, minutely hairy. Male flowers: calyx lobes ca. 0.8-0.9 × 0.6 mm, glabrous; petals ± obovate, 1.2-1.4 × 0.8-0.9 mm, apex rounded or emarginate, minutely ciliolate (at × 40); disc lobes 0.3-0.4 long, oblong or broadly oblong with thin flanges on either side of each lobe; filaments ca. 2.6-3 mm long; ovary minute, ca. 0.6 mm long, densely golden pubescent, styles 0.1-0.2 mm long, incurved. Fruit unknown.—Fig. 10, 11A-D.

JUVENILE FOLIAGE.—Non-reproductive (coppice ?) shoots: axes tomentose, internodes long, often ca. 8 cm. Stipules orbicular to reniform and shortly stalked, up to 1 × 1.2 cm. Leaves up to 11 cm long, almost perpendicular to stem (not ± erect as in adult foliage), lateral leaflets in 8-10 pairs, ± oblong, up to 2 × 0.8(-1) cm, chartaceous sometimes widely spaced on the rachis (not ± imbricate); rachis segments up to 0.9 cm. (See *Hoogland 12578*, *Siew Wei Hoe 15* and *Chiew Geok s.n.*). Juvenile leaves are longer than adult ones and have more pairs of leaflets.

BREEDING SYSTEM.—Probably dioecious, but female flowers have not been seen.

FIELD CHARACTERS.—The leaves are clustered towards the end of the twigs and held ± erect to form an even, dense, ball-like, congested crown (J.C. BRADFORD pers. obs.). Young branches and leaf rachises purplish or brown. Foliage dark green above, leathery. Flowers white on pink stalks (*Whitmore FRI 12582*), corolla and stamens white (*Ng FRI 6236*).

DISTRIBUTION AND ECOLOGY.—Known from mountains in western Peninsular Malaysia, from ca. 1680-2065 m. Habitats described as upper montane forest, moss forest and summit forest of low stature; locally common.

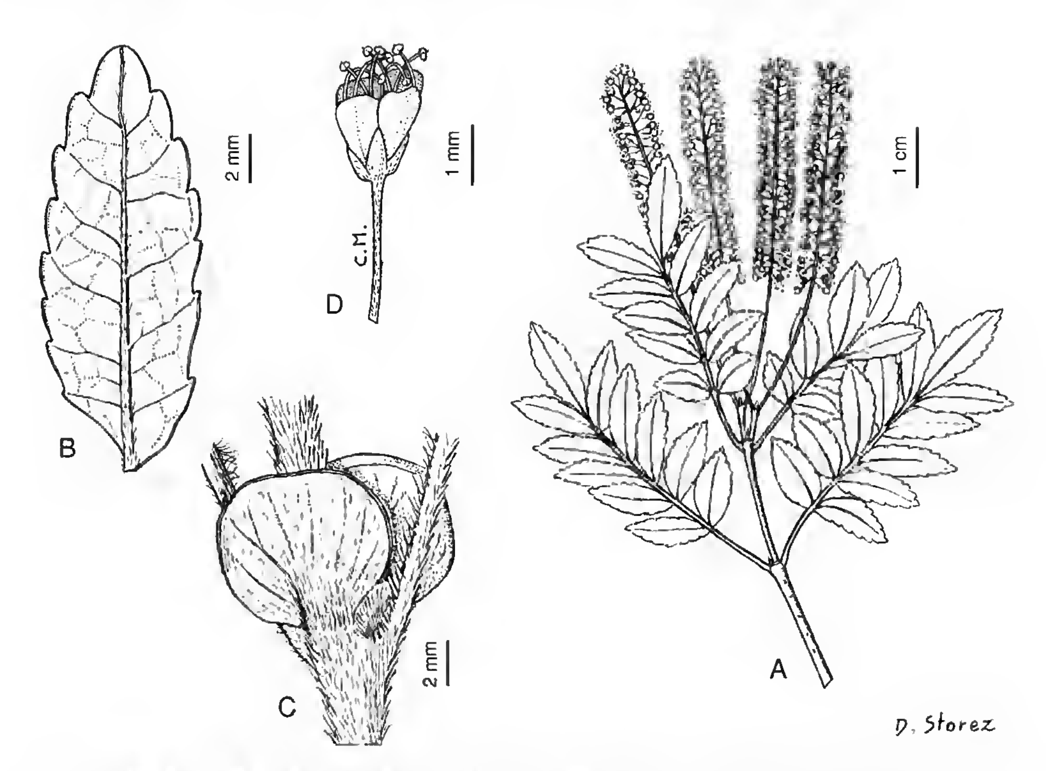


Fig. 11.—***Weinmannia hooglandii***: **A**, Flowering shoot showing inflorescence of two "dyads" (each of two racemes on a short peduncle) in opposite leaf axils at the most distal node of the shoot; **B**, Underside of a lateral leaflet; **C**, Node on a vegetative shoot showing a pair of stipules between opposite petioles with a sericeous bud in the axil of the right-hand petiole; **D**, Male flower, the filaments not fully extended. (A, B, D, *Whitmore FRI 12582*; C, *Bradford 580*).—Drawn by C. MONNIÉ and D. STOREZ.

MATERIAL EXAMINED.—PENINSULAR MALAYSIA: *Bradford 579, 580*, Pahang, Gn. Ulu Kali, Genting Highlands, 3°23'N-101°45'E, 1680 m, st., 18 Mar. 1996 (KEP, MO, P); *Chiew Geok s.n.*, Pahang, Genting Highlands, 5600 ft., st., 22 June 1974 (BISH); *Hoogland 12578*, Pahang, Summit Gn. Brinchang, 6300 ft., st., 1 Apr. 1975 (CANB); *Murdoch s.n.*, Selangor, Gn. Ulu Kali, st., 25 Mar. 1905 (K); *Ng FRI 6236*, Selangor, Summit Gn. Mengkuang, fl., 11 Jan. 1972 (KEP); *Siew Wei Hoe 15*, Gn. Ulu Kali, Genting Highlands, 5800 ft., st., 4 June 1977 (L); *Soepadmo & Suhaimi S172*, Gn. Ulu Kali, 3°27'N-103°48'E, 1772 m, st., 8 May 1990 (A); *Symington 32246*, Perak, Gn. Korbu F.R., Cameron Highlands, 5000-7000 ft., st., 22 July 1933 (KEP).

This species is named for R.D. HOOGLAND, specialist in the Cunoniaceae for over 35 years, who recognized his collection from Gunung Brinchang as "something interesting".

RELATIONSHIPS.—The material placed here in *Weinmannia hooglandii* had previously been regarded as a small-leafleted variant of the common and widespread *W. fraxinea* (D. Don) Miq. (synonym *W. blumei* Planch.) from high elevations. However, J.C. BRADFORD observed individuals of *W. hooglandii* growing next to *W. fraxinea* (with much larger, narrowly elliptical leaflets) at the same altitude and in the same habitat at Gn. Ulu Kali, Genting Highlands, in March 1996, suggesting that *W. hooglandii* is not merely an ecotype of the latter, and could be regarded as distinct. This observation is documented by *Bradford 578* and *581* (*W. fraxinea*) and *Bradford 579* and *580* (*W. hooglandii*).

Weinmannia hooglandii is distinguished from *W. fraxinea* by its smaller leaflets with more densely reticulate venation visible on the lower surface, and shorter internodes producing a congested, not diffuse, crown. The shape of the lateral leaflets is also different; in *W. fraxinea* in Peninsular Malaysia, the leaflets are usually lanceolate or narrowly elliptical [length to breadth ratio 1: 0.23-0.33(-0.38)] while in *W. hooglandii* distal leaflets are oblong or subfalcate (with the main vein asymetrically placed) or sometimes suboblanceolate (length to breadth ratio 1: 0.30-0.39) and the proximal ones broadly elliptical. In addition, the stipules in *W. hooglandii* are smaller, being up to 6 mm broad, while the smallest seen in *W. fraxinea* are 9 mm broad, though in many specimens they are not seen, having already fallen.

A further difference between *Weinmannia hooglandii* and *W. fraxinea* is the presence of supernumerary lateral buds at nodes, especially those bearing partial inflorescences, in the latter. Usually in *W. fraxinea* a reproductive node has two or three buds in each opposite leaf axil, and one, two or three pairs of partial inflorescences develop from them (each partial inflorescence being a dyad or a tetrad). In the few fertile specimens of *W. hooglandii* available, there is only one pair of buds at a reproductive node, and so the inflorescence that develops consists of a pair of dyads (Fig. 11A), as in *W. urdanetensis* (see below).

Although *Weinmannia hooglandii* and *W. fraxinea* can readily be distinguished from one another where they occur together, *W. fraxinea* is a complex and variable species that in some parts of its range has rather small leaves whose leaflets approach those of *W. hooglandii* in size [e.g. *Cockburn FRI 11030*, Peninsular Malaysia, Pahang, Summit Padang of Gn. Tapis, 4500 ft., fr., 11 Sep. 1968 (K, KEP, L); *Symington & Kiah SF 28894*, Pahang, Gn. Tapis, Kuantan, 4600 ft., fl., fr., 14 June 1934 (BO, SING)]. In these cases, leaflet shape and the venation are typical of *W. fraxinea*, and the leaflets are more widely spaced (not imbricate) along the rachis.

Weinmannia urdanetensis, which grows in montane forests in New Guinea and the Philippines, also has small leaflets, and like *W. hooglandii*, the inflorescence is typically a pair of dyads. Mature foliage of *W. hooglandii* differs from that of *W. urdanetensis* by its usually shorter leaves with fewer pairs of leaflets [4-8 not (2-)6-10(-19)], the leaves held at an acute angle to the stem in mature foliage (not more or less at right angles) and the leaflets positioned at an acute angle to the leaf rachis (not more or less at right angles).

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A revision of *Weinmannia* (Cunoniaceae) in Malesia and the Pacific. 2. Sulawesi and the Philippines

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ABSTRACT
Eleven species of *Weinmannia* occur in Sulawesi and the Philippines, but only one (*W. negrosensis*) is common to both regions. All species are placed in sect. *Fasciculata* although *W. descombesiana* shows some characteristics of sect. *Leiospermum*. Of the seven species from Sulawesi, four are described here as new: *W. devogelii* is closely related to *W. fraxinea*, the most wide-spread Malesian species which is absent from both Sulawesi and the Philippines; *W. furfuracea* also occurs in Seram; *W. coodei* and *W. eymaeana* are both endemic. The seventh species from Sulawesi, *W. celebica*, is rather poorly known. In the Philippines, five species are recognised, none of them new. *Weinmannia hutchinsonii*, *W. luzoniensis* and *W. lucida* are all endemic, *W. urdanetensis* occurs in both the Philippines and New Guinea, and the fifth species is *W. negrosensis*. Keys, illustrations and distribution maps are given.

KEY WORDS
Weinmannia,
Cunoniaceae,
Sulawesi,
Philippines.

RÉSUMÉ
Onze espèces de *Weinmannia* existent aux Célèbes et aux Philippines, mais une seule (*W. negrosensis*) est commune aux deux régions. Toutes les espèces appartiennent à la sect. *Fasciculata*, bien que *W. descombesiana* présente certaines affinités avec la sect. *Leiospermum*. Parmi les sept espèces des Célèbes, quatre sont nouvelles et décrites ici : *W. devogelii*, très affine de *W. fraxinea* qui est l'espèce la plus répandue en Malésie mais absente des Célèbes et des Philippines ; *W. furfuracea* qui existe aussi à Seram ; *W. coodei* et *W. eymaeana*, toutes deux endémiques. La septième espèce, des Célèbes, *W. celebica*, est assez peu connue. Cinq espèces existent aux Philippines, mais aucune n'est nouvelle. *Weinmannia hutchinsonii*, *W. luzoniensis* et *W. lucida* sont endémiques, *W. urdanetensis* se trouve à la fois aux Philippines et en Nouvelle-Guinée, la cinquième espèce étant *W. negrosensis*. Des clés de détermination, des illustrations et des cartes de distribution sont présentées.

MOTS CLÉS
Weinmannia,
Cunoniaceae,
Célèbes,
Philippines.

This is the second part of a revision of the Malesian-Pacific species of *Weinmannia*. Part 1 (HOPKINS 1998a) gives a general introduction, including definitions of the terms used for the structure of the inflorescence, and describes the species of western Malesia. Parts 3 and 4 (HOPKINS 1998b; HOPKINS & FLORENCE 1998) deal with the species of the western and central Pacific respectively.

Most of the *Weinmannia* species found in Sulawesi and the Philippines are clearly defined and monomorphic. Most are also endemic to one or other of these regions, though there is a marked difference in that all the taxa recognised here from the Philippines have been known for some time, while for Sulawesi, four species are described here as new, and incomplete material probably represents a fifth. Sulawesi has the highest number of sympatric *Weinmannia* species of any island (or island group) in Malesia, and further exploration of its montane forests might well be rewarding. Although all the species dealt with here belong to sect. *Fasciculata*, *W. descombesiana* from Sulawesi is noteworthy because it shows some characteristics of sect. *Leiospermum* (see below).

WEINMANNIA IN SULAWESI

Seven species are recognised from Sulawesi (Celebes), five of which are endemic (*Weinmannia celebica*, *W. coodei*, *W. descombesiana*, *W. devogelii* and *W. eymaeana*). All occur in montane forest with the exception of *W. devogelii*, which occurs in lowland forest up to 700 m. Two species have bisexual flowers (*W. descombesiana* and *W. furfuracea*), four have unisexual ones and for *W. coodei*, the breeding system is undetermined.

Key to the species in Sulawesi

1. Leaves simple (unifoliolate); flowers inserted singly in the axils of the bracts on the inflorescence axes .... **1. W. descombesiana**
1'. Leaves trifoliolate or imparipinnate (or rarely unifoliolate); flowers inserted in fascicles in the axils of the bracts on the inflorescence axes 2
2. Leaves 1-3 foliolate, coriaceous .... **7. W. negrosensis**
2'. Leaves usually with 5 or more leaflets, chartaceous to subcoriaceous 3
3. Lateral leaflets in 3-20 pairs, the largest per leaf 0.7-1.9 × 0.2-0.5 cm .... **4. W. eymaeana**
3'. Lateral leaflets in (0-)1-6 pairs, the largest per leaf ≥ 3 × 1 cm 4
4. Lateral leaflets elliptical to ovate, apex acuminate 5
4'. Lateral leaflets narrowly elliptical to obovate, apex obtuse or rounded 6
5. Pedicels 0.2-0.5 mm long at anthesis; lateral leaflets 4.5-10 × 1-3 cm; indumentum on young stems sparse and never pilose .... **2. W. devogelii**
5'. Pedicels 1.8-2 mm long at anthesis; lateral leaflets 3-5 × 1-1.6 cm; indumentum on young stems at least partly pilose .... **6. W. celebica**
6. Young stems and leaves, stipules, leaf rachises and inflorescence axes bearing a rusty or golden brown villous-tomentose indumentum .... **3. W. furfuracea**
6'. Young stems glabrous; leaf rachises glabrous or tomentose on adaxial side, inflorescence axes puberulous; indumentum neither rusty nor golden brown .... **5. W. coodei**

1. Weinmannia descombesiana Bernardi

Bot. Jahrb. Syst. 83: 190, t. 33 (1964).—Type: *Kjellberg 1618*, SW Sulawesi, Pasoei-Rante Lemo, 1000 m, fl., 9 June 1929 (holo-, S!; iso-, BO).

Shrub or tree, 2.6-30 m high, up to 30 cm dbh. Young stems glabrous or puberulous, black, shiny, older ones with numerous white lenticels; branching sometimes dichotomous. Stipules usually caducous, obovate, ligulate or spathulate, ca. 0.7 × 0.4 cm, apex rounded, abaxial surface shortly strigose especially towards the base, otherwise glabrous, adaxial surface glabrous. Leaves unifoliolate usually with an articulation between blade and petiole; petiole 0.5-1 cm long, semiterete and somewhat channelled, rarely winged, almost glabrous; leaf blades elliptical,

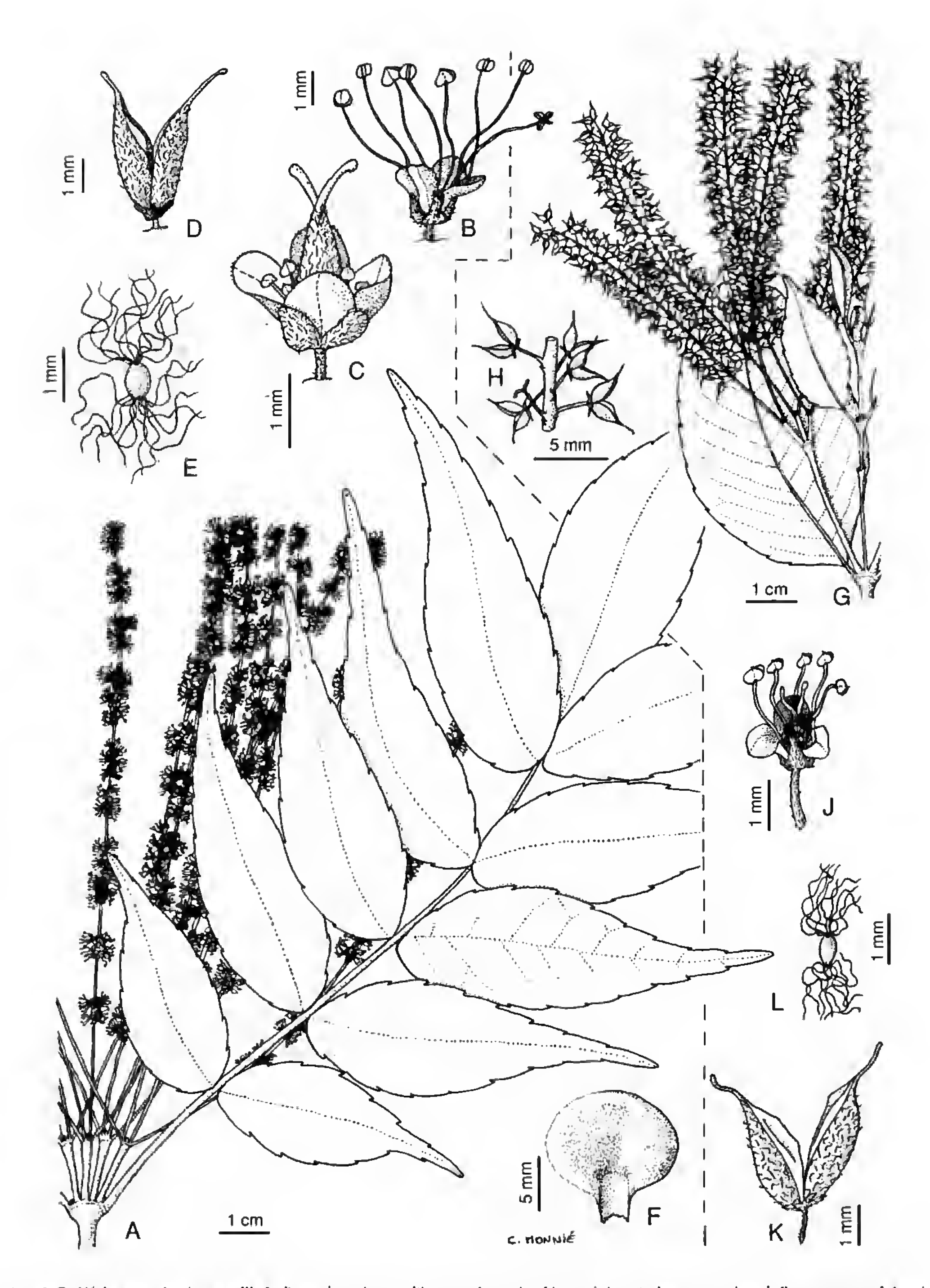


Fig. 1.—**A-F**, ***Weinmannia devogelii***: **A**, flowering shoot with one of a pair of imparipinnate leaves and an inflorescence of 4 pairs of tetrads; note minute buds in angle between the central racemes of each tetrad; **B**, male flower, styles too short to be visible; **C**, female flower with very short filaments; **D**, dehisced capsule; **E**, seed; **F**, stipule. (A, B, *Meijer 11147*; C, *de Vogel 5682*; D-F, *de Vogel 5959*).—**G-L**, ***Weinmannia descombesiana***: **G**, shoot showing infructescence developed from an axillary shoot bearing 3 dyads, the apical bud continuing to grow vegetatively; **H**, section of axis of a raceme showing pedicels of capsules inserted singly; **J**, bisexual flower; **K**, dehisced capsule; **L**, seed. (G, H, J, *bb 20870*; K, L, *bb 22981*).—Drawn by C. MONNIÉ.

4-9.5(-11) × 1.7-4.4(-4.8) cm, base acute, apex acuminate, subcoriaceous or chartaceous, glabrous on both surfaces, not punctate below; margin sometimes minutely thickened and revolute, crenate, ca. 8-19 crenations on each side; midrib flat or slightly depressed above, glabrous, prominent below with sparse indumentum, secondary and tertiary venation flat above and below, reticulum dense.

Inflorescence usually a pair of dyads, sometimes a few successive nodes producing partial inflorescences simultaneously; peduncles 0.2-1.6 cm long, sparsely puberulent; when inflorescence is at most distal node of stem, apical bud between the central pair of peduncles usually present and sericeous or rarely developed into a partial inflorescence; buds at apex of peduncle in angle between central pair of racemes sericeous, minute; axes of racemes puberulent, up to ca. 8.5 cm long. Floral buds inserted singly; floral bracts carinate, ca. 0.7 mm long, strigose-pubescent. Flowers bisexual; pedicel 1-1.2 mm long in flower, 1.4-2.6 mm long in fruit, almost glabrous; calyx lobes 0.5 × 0.4 mm, sparsely hairy on outer surface, ciliate; petals oblong, apex rounded, 1.2 × 0.6 mm, minutely ciliate; disc lobes 0.2-0.3 mm long, oblong, minutely strigose; filaments ca. 2.2 mm long; ovary ca. 1 mm long, densely pubescent; styles ca. 1 mm long, diverging; stigmas capitate, papillose.

Capsule 2-2.5 × 1.2-1.6 mm at dehiscence, the styles ca. 1 mm long, the exocarp strigose-pubescent; calyx lobes persistent; central column present and as long as valves. Seeds 0.5-0.6 mm long, ca. 8 per capsule, often persisting in capsules after dehiscence, comose at both ends, the hairs to 1.5 mm long, hairs almost "sticky".— Fig. 1G-L, 2.

Juvenile foliage.—Stipules suborbicular, not amplexicaul, up to 1.5 × 1.3 cm, persistent. Leaves elliptical, the petiole up to 1 cm long, the blade up to 17.5 × 6.3 cm, chartaceous, the margin with up to 20 notches on each side.

Breeding system.—Hermaphroditic.

Field characters.—Young leaves red or reddish purple. Buds pink or green, flowers white or pale green, smell faint; fruits yellow or green, turning red with age.

Distribution and ecology.—Mountains of South and Central Sulawesi, at 1000-1800 m. In primary and secondary forest on a variety of soil types.

Material examined.—**South Sulawesi**: *bb 20870*, Ond. afd. Mamasa, nabij Tandoeng, 1400 m, buds, fl., fr., 13 July 1936 (A, K, L); *bb 22981*, Ond. afd. Makale-Ratepao, nabij Tandoeng, 1150 m, fr., 17 July 1937 (A, BISH, BM, L, P); *bb 24206*, Ond. afd. Mamasa, nabij Limbong, 1500 m, yfr., 7 Apr. 1938 (A, L); *bb 26643*, Ond. afd. Masamba, nabij Tedeboë, 1800 m, fr., 25 Nov. 1938 (A, L); *Mamakit bb s.n.*, Ond. afd. Mamasa, nabij Mamasa, 1150 m, st., 2 Aug. 1941 (L); *Eyma 432*, Ond. afd. Enrekang, between Pasoei-Rante Lemo, 1330 m, st., juv., 14 June 1937 (L); *Eyma 3590*, Rec. Menado, Ond. afd. Poso, between Biv. III - Biv. IV, top Gn. Loemoet, fr., 4 Sep. 1938 (A, K, L).

Local names.—Paseh (language Toradja, dialect Tai), Panessean (Passe) (language Toradja), Londong (languages Toradja & Rongkong), Malètoea (language Rampi). Local uses: firewood.

This species was placed in sect. *Leiospermum* (*sub nom.* sect. *Racemosae*) by Bernardi (1964) because the flowers are arranged singly in the axils of the bracts on the axes of the racemes. However, it shows a mixture of characters of both sect. *Leiospermum* and *Fasciculata* as they are circumscribed in part 1 (Hopkins 1998a). Besides the insertion of the flowers, those characters seen in *Weinmannia descombesiana* that are indicative of sect. *Leiospermum* are: branching sometimes dichotomous; stipules ovate-ligulate-spathulate in adult foliage; free central column of capsules well developed.

However, the inflorescence structure is typical of sect. *Fasciculata*, and usually consists of a pair of dyads or tetrads with short, laterally flattened peduncles, that develop from axillary buds. When the dyads are at the most distal vegetative node of a shoot, there is usually an apical bud between them or rarely it may develop into a third dyad (see Fig. 1G); in some other cases the partial inflorescences are inserted in the axils of leaves at subdistal nodes. Other characters that suggest an affinity with sect. *Fasciculata* are the pubescent (not strigose) indumentum on the capsules, the calyx lobes persistent in fruit, and

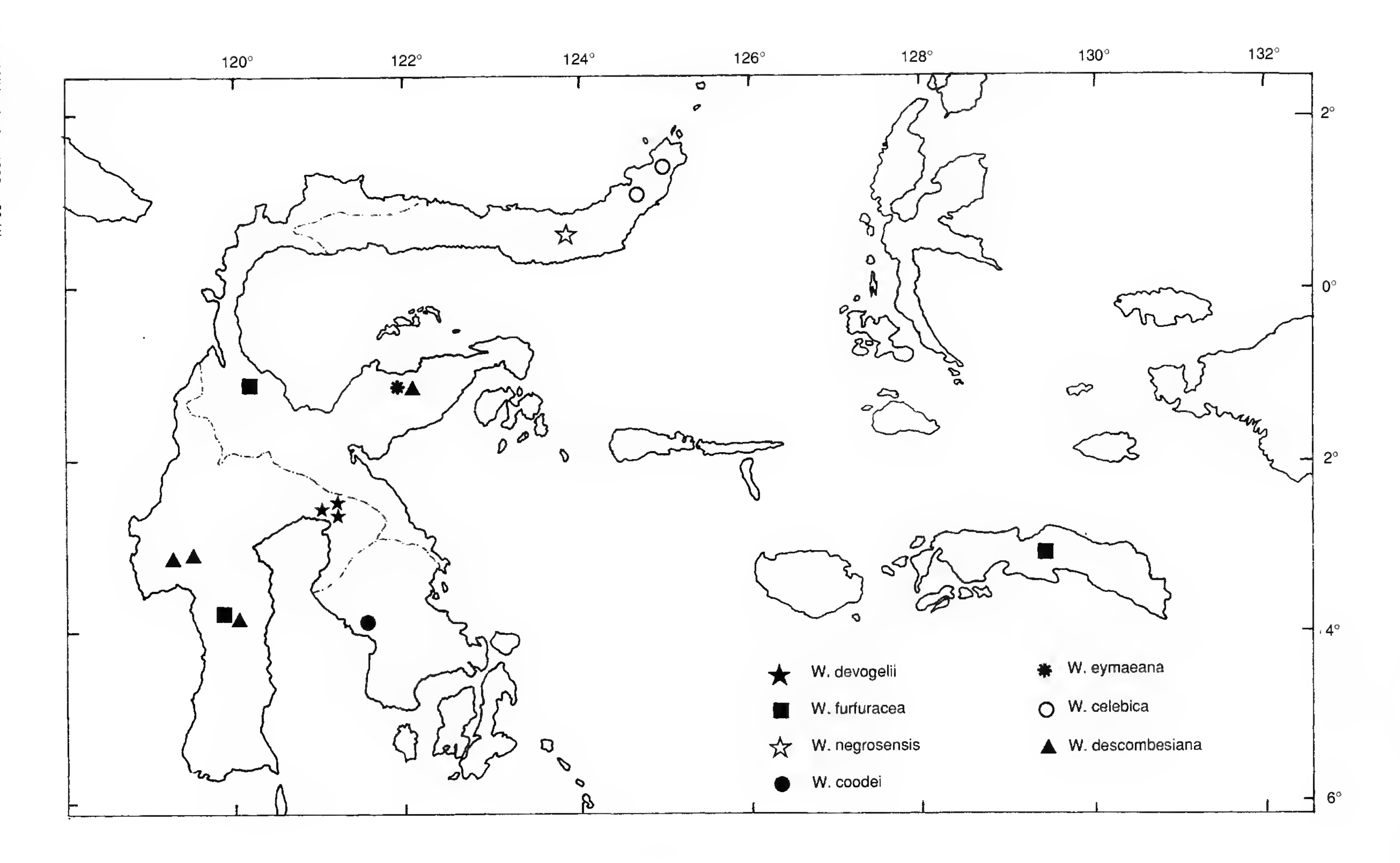


Fig. 2.—Distribution of ***Weinmannia*** in Sulawesi and Seram.

the absence of "collars", which are the remnants of a pair of partially fused, protective stipules, on the axes of the partial inflorescences, and which are seen frequently in sect. *Leiospermum*. A cladistic analysis based on morphology suggests that this species belongs in sect. *Fasciculata* (BRADFORD in press).

2. Weinmannia devogelii H.C. Hopkins, **sp. nov.**

A Weinmannia fraxinea (D. Don) Miq. *floribus subsessilibus (pedicellis 0.2-0.5 mm longis non (1.1-)1.5-3 mm) attingentibus roseis non albidis differt.*

TYPE.—*de Vogel 6122*, (South Sulawesi) Sulawesi Selatan, N shore of Lake Matano, Bonemaitu, E of Nuha, 2°20'S-121°27'E, 400 m, fl., 5 July 1979 (holo-, L!; iso-, K!).

Tree 5-20 m, up to 40 cm dbh. Young stems woody with sparse indumentum, older ones glabrescent with minute longitudinal fissures and numerous lenticels; branching not dichotomous. Stipules caducous or not, ± orbicular or larger ones amplexicaul, up to 1.4 × 1.6 cm, base usually constricted, apex rounded, adaxial surface glabrous, scurfy or puberulent, abaxial surface shortly strigose or glabrescent. Leaves imparipinnate, lateral leaflets (0-)2-6 pairs, total length up to 22 cm; petiole 1.5-3.5 cm long, rachis segments 1.2-2.5 cm long, petiole and rachis segments terete to semiterete, somewhat flattened and densely pubescent on adaxial side; indumentum sparse on abaxial side; lateral leaflets lanceolate, narrowly ovate or narrowly elliptical, the largest 4.5-10 × 1-3 cm, the base unequal, ± sessile or shortly petiolulate, apex acuminate; apical leaflet narrowly elliptical, ca. 5.5-9.5 × 1.5-2 cm, base attenuate into a petiolule ca. 0.7 cm long, apex acuminate; leaflet blades chartaceous to subcoriaceous, glabrous above and below, not punctate; margin almost entire to crenulate, 10-15 notches on each side of the largest lateral leaflets; midrib slightly depressed above, puberulent at base, prominent below and sparsely strigose, secondary and tertiary venation slightly raised on both surfaces, reticulum not dense.

Inflorescence of 1-3 pairs of dyads or tetrads, sometimes a few successive nodes producing partial inflorescences simultaneously; peduncles laterally flattened, 0.2-1.3 cm long, puberulous; bud(s) between the central pair of peduncles sericeous; buds at apex of peduncle in angle between central pair of racemes sericeous, minute; axes of racemes densely puberulous, up to 11.5 cm long. Floral buds inserted in fascicles; floral bracts ± carinate, ca. 0.8 mm long, minutely strigose, caducous. Flowers unisexual; pedicel 0.2-0.5 mm long, minutely strigose or puberulous; calyx lobes 0.5-0.7 × 0.4-0.5 mm, minutely strigose on outer surface; corolla obovate, 1.1-1.5 × 0.7-1.1 mm, apex rounded or irregularly emarginate, ciliate; disc lobes 0.2-0.3 mm long, oblong; in male flowers: filaments 3.3-3.7 mm long, ovary 0.4-0.5 mm long, pubescent, styles 0.1-0.2 mm long, incurved; in female flowers: filaments 0.6-0.9 mm long, ovary 0.9-1.1 mm long, densely pubescent, styles 0.9-1.1 mm long, straight, stigmas papillose.

Capsule 1.9-2.5 × 1.2-1.5 mm at dehiscence, the styles up to 1 mm long, the exocarp pubescent; calyx lobes persistent; central column present. Seeds ellipsoid to broadly ellipsoid, 0.5-0.7 mm long, 4 per capsule, comose at both ends, the hairs to 2 mm long.—Fig. 1A-F, 2.

BREEDING SYSTEM.—Dioecious.

FIELD CHARACTERS.—Buttresses few or absent. Outer bark ochre-grey, fissured or not; inner bark reddish; sapwood cream coloured; heartwood very hard, reddish. Young leaves red. Flower buds red; flowers usually given as pink, rarely white and fragrant (*Waturandang 18*); young fruit reddish green, old ones dark red.

DISTRIBUTION AND ECOLOGY.—Eastern South Sulawesi near Malili and Lake Matano at 0.5-700 m. In primary and secondary forest, including disturbed primary forest with an undergrowth of sedges and ferns. On peridotite and ultrabasic laterite; also in patches of coastal vegetation along the lake on limestone and alluvium derived from limestone and schist, and on red clayey soil derived from conglomerate bedrock. Locally common.

PARATYPES.—SOUTH SULAWESI: *van Balgooy 3625*, Soroako-Wasuponda road, 2°15'-3°S, 121°-121°45'E,

600 m, fl., 9 July 1979 (A, K, L); *van Balgooy 3809*, Soroako-Malili road nr. junction with road to Larona Hydroelectric plant, 2°15'S-121°45'E, 100 m, fl., 29 June 1979 (A, K, L); *Darnaedi 2236*, 2°15'-3°S, 121°-121°45'E, 500 m, fl., 14 July 1979 (A, K, L); *Meijer 11147*, Matano Lake nr. Soroako, NE of Malili, E of Nuha village, 2°35'S-121°20'E, fl., 15 July 1976 (L); *Meijer 11181*, Matano Lake nr. Soroako, NE of Malili, nr. old Mining office, 2°35'S-121°20'E, yfr., 16 July 1976 (L); *Ramlanto 138*, Wae Atue, Manurung 7 km from Malili, 5 m, fl., 10 Apr. 1984 (A, K, L); *Reppie 392, Cel.IIII-18*, Ond. afd. Malili; nabij Oesoe, fr., 11 Mar. 1935 (A, BO); *Schmid 5512*, Soroako, 500 m, buds, Jan. 1979 (L, P); *de Vogel 5682*, S of Lake Matano, ca. halfway between Soroako and Wasupondo, 2°31'S-121°21'E, 700 m, fl., 10 June 1979 (K, L); *de Vogel 5959*, S shore of Lake Matano W of Soroako and Taipa, on and nr. Pulau Lintu, 2°29'S-121°15'E, 400 m, fr., 23 July 1979 (K, L); *Waturandang 18, Cel.IIII-18*, Ond. afd. Malili, nabij Oesoe, 0.5 m, st., 14 Oct. 1931 (BO, K, L).

LOCAL NAMES.—Poémé (Tobela language, dialect To Pado E).

Weinmannia devogelii is a satellite of the widespread and variable *W. fraxinea*. While the differences between the two are not great, the first is considered here to be more than a mere variety of the second because it has a unique morphological feature (the very short pedicel) that is not seen in *W. fraxinea*, a distinctive ecology, and an allopatric distribution. However, the leaf characters of *W. devogelii* fall within the range for *W. fraxinea* and sterile specimens cannot be distinguished; the latter species is assumed to be absent from Sulawesi as no fertile material can be identified as belonging to it (unless *Kjellberg 2950* (BO) [Todjamboe, 700 m, tree 10 m; flowers male; leaflets 3-5 per leaf] proves to be it). The flowers are usually pink in *W. devogelii* and usually white in *W. fraxinea* at low altitude.

This species is named after E.F. DE VOGEL who collected the type. The prefix "de" is included in the epithet on purpose.

3. Weinmannia furfuracea H.C. Hopkins, sp. nov.

Weinmannia devogelii H.C. Hopkins *affinis, sed foliolorum indumento furfuraceo, nunquam glabra, apicibus juvenalibus indumento villoso-tomentoso, non breviter pubescente et foliolis ellipticis vel obovatis apice rotundato vel obtuso, non ovatis apice acuminato, praecipue differt.*

TYPE.—*Tantra 1595*, Central Sulawesi, 0°30'-1°30'S, 119°30'-120°30'E, W slope Mt. Roroka Timbu, SE of Palu, primary forest, 2000 m, fl., 5 May 1979 (holo-, L!; iso-, BO).

Tree 16-45 m high, up to 60 cm dbh. Young stems and leaves, stipules, leaf rachises and inflorescence axes covered with dense rusty or golden brown villous-tomentose indumentum, the longest hairs up to 1 mm; older stems tomentose or puberulous, finally glabrescent with longitudinal fissures and numerous lenticels; branching not dichotomous. Stipules caducous except at growing tips and in immature foliage, ± orbicular, recurved, up to ca. 0.9 × 1.1 cm, base constricted, apex rounded, abaxial surface tomentose-villous, adaxial one velutinous. Leaves imparipinnate with (1-)2-4 pairs of lateral leaflets, total length up to 20 cm; petiole 1-4 cm long, rachis segments 1-3.2 cm long, petiole and rachis segments terete to semiterete at point of insertion of leaflets where somewhat flattened on adaxial side, villous-tomentose; lateral leaflets elliptical to obovate, the largest per leaf 4-7.8 × 1.9-3 cm, the base almost equal, ± sessile or shortly petiolulate, apex rounded or obtuse (acute in immature foliage); apical leaflet elliptical to obovate, 5-9 (-11) × 1.9-3.6(-4.8) cm including base attenuate into a petiolule ca. 1 cm long, apex rounded or obtuse; leaflet blades subcoriaceous, glabrous above, with an indumentum of short, scurfy hairs below, sometimes glabrescent, not punctate; margin subentire to crenulate, 20-25 notches on each side of the largest lateral leaflets; midrib ± flat above, prominent below and bearing villous to scurfy hairs, secondary and tertiary venation ± flat above and somewhat raised below, reticulum fairly dense.

Inflorescence 1 or 2 pairs of dyads or tetrads, the apical bud between the central peduncles often continuing to grow vegetatively during flowering, sometimes a few successive nodes producing partial inflorescences simultaneously; peduncles laterally flattened towards apex, 0.6-2.5 cm long, villous-tomentose; apical buds between the central pair of peduncles and buds at

apex of peduncles in angle between central pair of racemes sericeous; axes of racemes tomentose, up to 11.5 cm long. Floral buds inserted in fascicles; floral bracts not seen. Flowers bisexual; pedicel 1-1.7 mm long, tomentose; calyx lobes 0.7 × 0.5-0.6 mm, tomentose on outer surface; corolla irregularly obovate to almost circular, 1-1.2 × 0.8-1 mm, apex rounded or irregularly emarginate, puberulous on outer surface, margin ciliate; disc lobes 0.3-0.4 mm long, oblong, sometimes with thin flanges on either side to form an almost continuous disc; filaments 2.2-2.4 mm long; ovary 1.1-1.8 mm long, densely pubescent; styles 1.1-1.8 mm long, divergent then later straight; stigmas capitate, papillose.

Capsule 3-4 × 1.5 mm before dehiscence, the styles up to 1.5 mm long, the exocarp densely pubescent; calyx lobes persistent. Immature seeds 0.6-0.8 mm long, comose at both ends.—Fig. 2, 3A-D.

Breeding system.—Hermaphroditic.

Field characters.—Tree without buttresses. Living bark dark brown, wood yellowish, heart wood light brown. Leaves golden from below, young leaves brown, old ones glaucous below. Flower buds greenish white, flowers white, fragrant, full of bees (*Tantra 1595*). Immature fruits yellowish green.

Distribution and ecology.—Mountains of Sulawesi and Seram. Primary forest at 1700-2000 m, including montane forest dominated by *Agathis* (up to 40 m tall) and in forest dominated by *Castanopsis* with *Trimenia*, *Eugenia*, *Phyllocladus*, Ericaceae and *Pandanus*. Locally common.

Paratypes.—**Central Sulawesi**: *van Balgooy 3255*, 0°30'-1°30'S, 119°30'-120°30'E, Mt. Roroka Timbu, W slope, 2000 m, fl., 10 May 1979 (A, L); *van Balgooy 3464*, 0°30'-1°30'S, 119°30'-120°30'E, Danau Tambing, 1700 m, fr., 23 May 1979 (A, L); *Tantra 1587*, W slope Mt. Roroka Timbu, SE of Palu, 0°30'-1°30'S, 119°30'-120°30'E, 2000 m, st., juv., 5 May 1979 (L); *Zijll de Jong 114/V2, bb 20787*, Ond. afd. Enrekang, Sawito, 1000 m, fl., 14 June 1936 (BO).—**Seram**: *Rutten 2231*, Mid Seram, Brongebergte Makina, ± 1000-1100 m, buds, 18 May 1919 (BO, L).

Local names.—Boeloean laki (language Buegin, Dialect Maiwa), Ula (language Uma).

Another specimen from western Seram with much smaller leaflets is close to this species (Tanah goyang, *Eyma 3008* [K, L, P]) but differs by being a large shrub rather than a tree, with unisexual not bisexual flowers. It also resembles *W. fraxinea* but that species lacks long, coarse, dense hairs.

4. **Weinmannia eymaeana** H.C. Hopkins, **sp. nov.**

Weinmannia urdanetensis Elmer *affinis, sed petiolis rhachidibusque canaliculatis anguste alatis et glabris, nec teretibus nec dense velutinis, foliolis ellipticis basi cuneato non oblongis basi truncato vel cordato et seminibus comosis utrinque, non hirsutis ubique, praecipue differt.*

Type.—*Eyma 3578*, Central Sulawesi, Res. Menado; Ond. afd. Poso, Tusschen, Biv. II-III, op N uitlooper van Gn. Loemoet, fl., fr., 3 Sep. 1938 (holo-, L!; iso-, A!, BO!, K!, U).

Shrub? Stems glabrous, bearing numerous pale lenticels. Branching not dichotomous. Stipules often persistent especially at flowering nodes, ± orbicular, up to 0.8 × 0.8 cm, narrowing at base, apex rounded, glabrous on both surfaces. Leaves imparipinnate, 3-20 pairs of lateral leaflets, total length up to 6 cm long; petiole and rachis segments 0.3-0.6 cm long, glabrous, channelled above, narrowly winged, the wings extending 0.5 mm on either side of midline and incurved; lateral leaflets narrowly elliptical or elliptical, (0.45-)0.7-1.9 × 0.2-0.5 cm, of ± equal size in one leaf, the largest often near the midpoint of the rachis, base sessile, ± equal, cuneate, apex acute; terminal leaflet narrowly elliptical to elliptical, 0.7-2.3 × 0.25-0.8 cm, scarcely larger than the largest laterals, base sessile or petiolulate, the petiolule ca. 0.3 cm long, apex acute; blade glabrous, coriaceous, cuticle on upper surface thick and shiny, not punctate below; margin recurved, entire or sparsely crenate-dentate with 0-7 notches on each side in the lateral leaflets; on upper surface, midrib and secondary veins depressed into cuticle and tertiary venation obscure; on lower surface, midrib somewhat prominent.

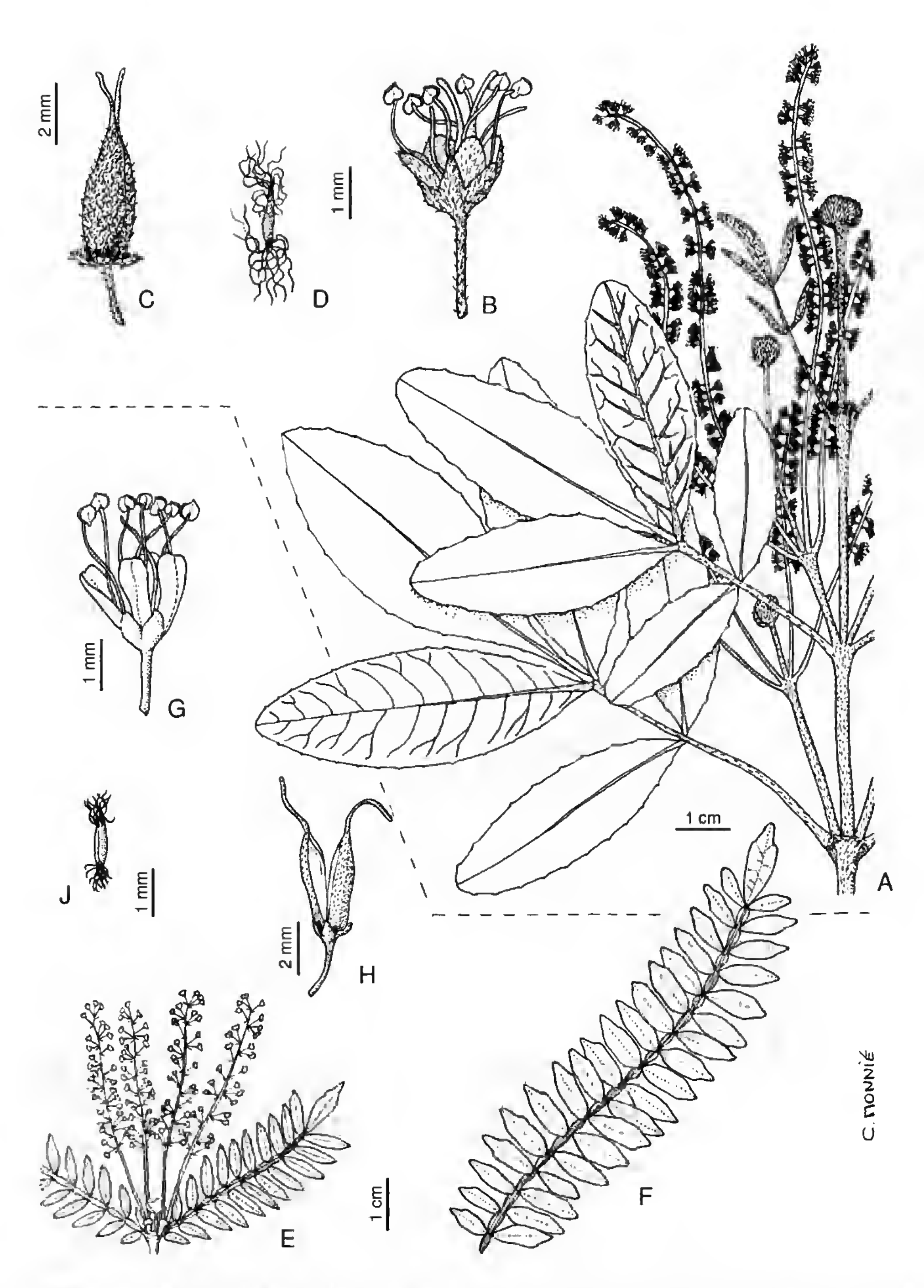


Fig. 3.—**A-D *Weinmannia furfuracea***: **A**, flowering shoot showing 2 lateral tetrads in sequential leaf axils where in both cases, the bud between the central racemes is continuing to grow vegetatively; the apical bud of the shoot is also continuing to grow vegetatively; **B**, bisexual flower; **C**, fruit just before dehiscence; **D**, seed. (A, B, *Tantra 1595*; C, D, *van Balgooy 3464*).—**E-J**, ***Weinmannia eymaeana***: **E**, flowering shoot showing an inflorescence of a pair of dyads; note apical bud between peduncles of dyads starting to develop; **F**, leaf with narrowly winged rachis; **G**, male flower; **H**, dehisced capsule; **J**, immature seed. (E-J, *Eyma 3578*).—Drawn by C. Monnié.

Inflorescence a pair of opposite dyads; apical bud glabrous, sometimes continuing to grow vegetatively during flowering and sometimes more than one node on a shoot producing dyads simultaneously; peduncles 0.1-0.3 cm long, racemes up to 8 cm long, small bud present in angle between racemes at apex of peduncle, glabrous; peduncles ± glabrous, axes of racemes puberulent; bracts at apex of peduncle persistent, ± triangular. Flowers inserted in fascicles; floral bracts carinate, sparsely hairy on abaxial surface, up to 1 mm long, sometimes persistent; flowers apparently unisexual, only male flowers seen: pedicel 1-2.3 mm long, glabrous or puberulent; calyx lobes 0.7 × 0.5 mm, glabrous; petals oblong, 1.4-1.6 × 0.6 mm, ± emarginate at apex; disc lobes 0.3 mm long, narrowly oblong; filaments up to 2.9 mm long; ovary ca. 0.4 mm long, pubescent; styles 0.1 mm long, incurved.

Capsules 3.5-4 × 1.8 mm plus style up to 2.2 mm long (just prior to dehiscence), the exocarp densely pubescent; calyx lobes and disc lobes persistent; central column about half the length of the valves and weakly developed. Seeds immature, flat, ca. 0.6 mm long, comose at both ends.—Fig. 2, 3E-J.

BREEDING SYSTEM.—Polygamodioecious? Male flowers and fruits present on *Eyma 3578* but not on the same twig.

FIELD CHARACTERS.—Stems and pedicels red, flowers pinkish white.

DISTRIBUTION AND ECOLOGY.—Endemic to Sulawesi and known from only 2 collections, both from Gn. Lumut (Loemoet). *Eyma 3607a* was collected on the top of Gn. Loemoet, and therefore at about 2200 m.

PARATYPE.—SULAWESI: *Eyma 3607a*, Res. Menado, Ond. afd. Poso, Tusschen Biv. III-Biv. IV, top Gn. Loemoet, fl., 4 Sep. 1938 (BO).

Eyma 3578 was included by BERNARDI (1964) in *Weinmannia urdanetensis* and appears to be the basis for his Tab. 29 (except g), but its similarity to *W. urdanetensis* is only superficial. The leaves of *W. eymaeana* are in fact more similar to those of *Pancheria multijuga* Guillaumin from New Caledonia. As sometimes occurs in other species of *Weinmannia*, the leaflet blades and calyx lobes are pustulate.

5. **Weinmannia coodei** H.C. Hopkins, **sp. nov.**

A Weinmannia furfuracea H.C. Hopkins *caulibus juvenibus glabris, non villosis-tomentosis, et foliolorum pagine abaxiali glabra non furfuracea recedit.*

TYPE.—*Coode 6197*, Sulawesi Tenggara (SE Sulawesi), Koaka area, 3°34'S-121°40'E, Gn. Watuwila foothills above Sanggona, Gn. Sopura, 1600 m, fr., 5 Nov. 1989 (holo-, L!; iso-, A!, K!).

Small tree 6 m high, 35 cm dbh. Young stems glabrous, ridged, nodes thickened with annular leaf scars prominent, older stems with longitudinal fissures and numerous white lenticels; branching not dichotomous. Stipules not seen, caducous. Leaves imparipinnate, with (1-)2 pairs of lateral leaflets, total length up to 13 cm; petiole 1.4-2 cm long, rachis segments 1-1.5 cm long, petiole and rachis segments semiterete and flattened or channelled and glabrous or tomentose on adaxial surface; lateral leaflets narrowly elliptical, distal leaflets larger than proximal ones, the largest per leaf 4.8-6.4 × 1.4-2.1 cm, the base unequal, ± sessile, acute, apex acute to obtuse; apical leaflet elliptical to obovate, 5-6.2 × 1.4-2.3 cm including base attenuate into a petiolule ca. 1 cm long, apex obtuse; blades subcoriaceous, glabrous above and below, not punctate; margin crenulate, 9-18 notches on each side of the largest lateral leaflets; midrib indented above, prominent below and glabrous, secondary and tertiary venation ± flat above and somewhat raised below, reticulum ± dense.

Inflorescence a pairs of dyads; peduncles up to 1 mm long, glabrous, the pair of stipules at the apex of the peduncle sericeous and persistent, and partially fused at their lateral margins to form a cup-shaped structure (Fig. 4A'), each stipule rounded at apex, abaxial surface strigose, adaxial surface glabrous; buds at apex of peduncles in angle between central pair of racemes not seen; axes of racemes puberulous, up to 7.5 cm long. Floral buds inserted in small fascicles; floral bracts ca. 0.7 mm long, carinate, pilose on outer surface. Flowers with pedicel 1-

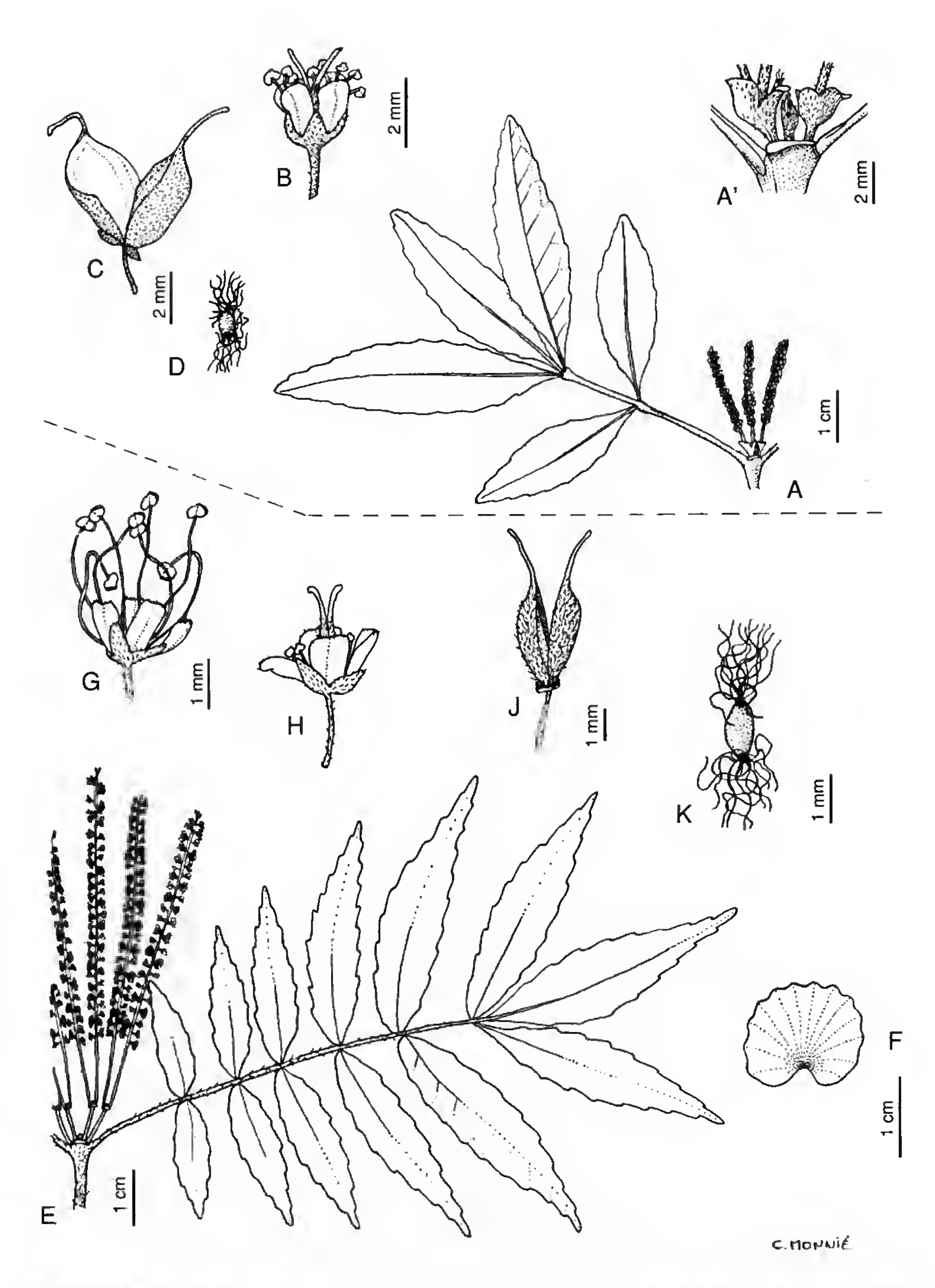


Fig. 4.—**A-D**, ***Weinmannia coodei***: **A**, shoot with one of a pair of opposite leaves and a developing inflorescence of 3 racemes; **A'**, enlargement of shoot apex (A) showing opposite petioles and scar from base of interpetiolar stipules, dormant apical bud in centre, and in axillary positions, between the apical bud and the petioles, the cupped bracts from within which the racemes arise (as 2 dyads with one raceme missing?); **B**, flower; **C**, capsule at dehiscence; **D**, seed. (A-D, *Coode 6197*).—**E-K**, ***Weinmannia hutchinsonii***: **E**, flowering shoot showing an inflorescence of 4 dyads; **F**, stipule; **G**, male flower; **H**, female flower; **J**, capsule at dehiscence, note persistent disc lobes but calyx lobes fallen; **K**, seed. (E, F, J, K, *Sulit PNH 2781*; G, *Elmer 14228*; H, *Elmer 17293*).—Drawn by C. MONNIÉ.

1.5 mm long, puberulous; calyx lobes 0.7 × 0.6 mm, pubescent on outer surface; corolla irregularly obovate to oblong, 1.4 × 0.8 mm, apex rounded, margin minutely ciliate; disc lobes 0.3-0.4 mm long, oblong or sometimes fused into an almost continuous disc; filaments up to 1.6 mm long; ovary 0.5-0.7 mm long, densely pubescent; styles 1.3 mm long, straight; stigmas capitate, papillose.

Capsule 3.5-4 × 2 mm at dehiscence, the styles 1.5-1.8 mm long, the exocarp densely pubescent; calyx lobes persistent. Immature seeds 0.6-0.8 mm long, either comose at both ends or with hairs all over surface, longest at ends.—Fig. 2, 4A-D.

BREEDING SYSTEM.—Not determined.

FIELD CHARACTERS.—Flowers pink with white stamens.

DISTRIBUTION AND ECOLOGY.—Known only from the type, from the SE peninsula of Sulawesi, from mossy ridge forest at 1600 m, on schist substrate with deep leaf-litter, canopy at 6 m; associates include *Pandanus*.

This species is named after Mark J.E. COODE who collected the type.

6. Weinmannia celebica Koord.

Meded. Lands Plantentuin. 19: 640 [450] (1898); Koord.-Schum., Syst. Verz. 3: 51 (1914); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Bernardi, Bot. Jahrb. Syst. 83: 165 (1964).—Type: *Koorders 18022b*, North Sulawesi, Residentie Menado, Loeloemboelan nr. Pahoe oere, 700 m, 8 Apr. 1895 (lecto-, here designated, BO!; isolecto-, BO!, L!).

Tree 5-27 m, up to 45 cm dbh. Young stems woody, pilose, the hairs up to 0.5 mm long, older stems more sparsely pilose to glabrescent with minute longitudinal fissures and numerous lenticels. Stipules few in mature foliage, suborbicular, up to 0.45 cm diameter, base constricted, abaxial surface strigose especially at base. Leaves imparipinnate with 3-6 pairs of lateral leaflets, total length up to 14 cm; petiole 1.5-2 cm long, rachis segments 0.8-1.1 cm long, petiole and rachis segments semiterete, somewhat flattened on adaxial side, pilose and/or puberulent, often densely so on adaxial side; lateral leaflets lanceolate or narrowly elliptical, the largest 3-5 × 1-1.6 cm, the base unequal, ± sessile, apex acuminate; apical leaflet narrowly elliptical, 5.2-7 × 1.4-2 cm, base attenuate into a petiolule ca. 0.7 cm long, apex acuminate; leaflet blades chartaceous to subcoriaceous, glabrous above, pilose below, not punctate; margin crenulate, 11-14 notches on each side of the largest lateral leaflets; midrib slightly depressed above, puberulent at base, prominent below and pilose, secondary and tertiary venation slightly raised on both surfaces, reticulum not dense.

Inflorescence a pair of dyads; peduncles laterally flattened, ca. 1 cm long, strigose-puberulous; apical bud between the central pair of peduncles sericeous; bud at apex of peduncle in angle between central pair of racemes sericeous, minute; axes of racemes puberulous, up to 11 cm long. Flowers inserted in fascicles; floral bracts ± ligulate, ca. 1.3 × 1 mm, minutely strigose, mostly caducous; flowers probably unisexual; pedicel 1.8-2 mm long, puberulous to glabrous; in old female flowers/young fruit: calyx lobes 0.8 × 0.6 mm, glabrous; corolla oblong, ca. 1.5 × 0.8 mm, apex rounded; disc lobes 0.2 mm long, oblong; filaments 1.6 mm long; ovary 1.2 mm long, densely pubescent; styles 1.3 mm long, straight or divergent; stigmas papillose. Mature fruits not seen.—Fig. 2.

JUVENILE FOLIAGE.—Stipules orbicular to amplexicaul, up to 1.2 × 1.1 cm, persistent. Leaves imparipinnate, up to 30 cm long, lateral leaflets in up to 16 pairs, to 5.2 × 1.4 cm, blades chartaceous, margin distinctly serrate.

BREEDING SYSTEM.—Probably dioecious.

FIELD CHARACTERS.—Young leaves red; flowers dirty white.

DISTRIBUTION AND ECOLOGY.—Known from the northern peninsula of Sulawesi around Menado in forest at 600-1500 m. Scarce to locally common.

MATERIAL EXAMINED.—**NORTH SULAWESI:** *Koorders 18017b*, Residentie Menado, Lolomboelan, 900 m, st., 12 Mar. 1895 (BO, L); *Koorders 18021b*, Gn. Klabat, 600 m?, st., juv., 19 Jan. 1895 (BO); *Koorders 18023b*, Oerwoud Lolomboelan bij Pakoe-Oere, 700 m, st., juv., 6 Apr. 1895 (BO); *Koorders 18025b*, Sapoetan-

gebergte, 1500 m, st., juv., 5 May 1895 (BO).

LOCAL NAMES.—Teregkoese.

Of the five collections cited by KOORDERS-SCHUMACHER, only one is fertile and three are of juvenile foliage. This species is distinguished from *W. fraxinea* by the pilose indumentum on the underside of the leaflets and from *W. devogelii* by the longer pedicels. Its affinities seem to be with *W. hutchinsonii* and *W. luzoniensis* from the Philippines but better collections are needed to determine whether it is in fact worthy of specific rank.

BERNARDI (1964) cited 2 collections for this species [*Neth. Ind. For. Serv. bb 20787* (A) from Sulawesi and *Rutten 2231* (U) from Seram] but did not see the type. Both of these specimens are now placed in *W. furfuracea*.

7. Weinmannia negrosensis Elmer

For synonomy and description, see under Philippines (p. 62).

MATERIAL EXAMINED.—NORTH SULAWESI: *Milliken 1034X*, Dumoga Bone National Park, Distr. Bolaang-Mongondow, nr. Gn. Sinombayuga, 0°28'N-123°44'E, 1970 m, fl., 25 Sep. 1991 (K).

FIELD NOTES.—Common, multi-stemmed tree in mossy montane forest; bark white, inner bark orange-brown turning bright orange; wood white. Petals and anthers white; pedicel, calyx and pistil pink.

Uncertain and little known species

Weinmannia sp. (Sulawesi A)

Monod de Froideville 119, South Sulawesi, afd. Mandur, Mt. Mamboeliling, N of Mamasa, 2700 m, st. (BO, L). Although placed by LAM (1945) in *Weinmannia urdanetensis*, its leaves are quite different, the leaflets being broader, petiolulate, and with the margin more sinuate.

Shrub or small tree; young stems densely pubescent, branching not dichotomous. Stipules ± orbicular, up to 0.6 mm wide, apex rounded, adaxial surface glabrous, abaxial one strigose, especially towards the base. Leaves imparipinnate with 9-11 pairs of leaflets, leaves up to 6 cm long; petiole and rachis segments terete, densely pubescent. Leaflets oblong or somewhat ovate, 0.7-1.1 × 0.5-0.6 cm, the terminal leaflet not markedly differing from the laterals in size or shape, base petiolulate, the petiolule ca. 0.5 mm long, apex obtuse; blades subcoriaceous, glabrous above and below except for strigose indumentum on midrib below; margin crenate-sinuate with 3-4 notches on each side of a leaflet. Flowers and fruits not known.

WEINMANNIA IN THE PHILIPPINES

Five species occur in the Philippines, three of which are endemic. The two which also occur outside the Philippines are *Weinmannia negrosensis* (also in Sulawesi) and *W. urdanetensis* (also in New Guinea). The most widespread Malesian species, *W. fraxinea*, has not been recorded from this region. Except for a small number of recent collections, field notes are often poor and thus it is difficult to judge whether the apparent ecological differences between species have any significance.

For several of the names published by ELMER and by MERRILL, the protologues do not specify where the holotype is located. According to VAN STEENIS-KRUSEMAN (1950), the first sets for these authors should be in Manilla. However, although the herbarium at PNH was destroyed during the Second World War (HOLMGREN et al. 1990), some ELMER types for names in *Weinmannia* are still extant there (unpublished notes of R.D. HOOGLAND at P). In these instances, the sheets at PNH are provisionally cited as holotypes. Where a specimen is not known from PNH, the collections seen or known to exist are listed as isotypes, and I have refrained from designating lectotypes because I have not had the opportunity to visit PNH and verify that no other type material is there.

The four species with medium-sized leaflets (*Weinmannia hutchinsonii*, *W. negrosensis*, *W.*

luzoniensis and *W. lucida*) appear closely related to one another. Characters that they share include: calyx lobes frequently falling in fruit (which is unusual in sect. *Fasciculata*); disc lobes short, broad and persistent in the fruiting stage; flowers unisexual; capsules densely pubescent; inflorescences often richly developed; stipules often persistent.

Key to the species in the Philippines

1. Leaves imparipinnate, the lateral leaflets 5-11 pairs, small (0.7-1.5 × 0.25-0.45 cm) .... **5. W. urdanetensis**
1'. Leaves simple, trifoliolate or imparipinnate, the lateral leaflets up to 7 pairs, the leaves or largest lateral leaflets per leaf 2-15.5 × 0.6-6.5 cm 2
2. Young stems and leaf axes pilose 3
2'. Young stems and leaf axes usually glabrous or if indumentum present, puberulent not pilose 4
3. Lateral leaflets (3-)5-7(-8) pairs, terminal leaflet 4.1-8.3 × 0.9-2.3 cm; length : breadth ratio for largest lateral leaflets per leaf 1 : 0.2-0.3 .... **1. W. hutchinsonii**
3'. Lateral leaflets 2-3(-4) pairs, terminal leaflet 6.7-12 × 2.2-5 cm; length : breadth ratio for largest lateral leaflets per leaf 1 : 0.33-0.52 .... **2. W. luzoniensis**
4. Leaves simple or trifoliolate, the blades coriaceous, elliptical or obovate, reticulum often dense .... **3. W. negrosensis**
4'. Leaves imparipinnate, (1-)2-3 pairs of lateral leaflets, blades subcoriaceous, elliptical, reticulum lax .... **4. W. lucida**

1. Weinmannia hutchinsonii Merr.

Philipp. J. Sci. Bot. 2: 275 (1907); Merr., Enum. Philipp. Fl. Pl. 2: 224 (1923); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Bernardi, Bot. Jahrb. Syst. 83: 169, t. 20 (1964).—Type: *Merrill 5753*, Philippines, Mindoro, Mt. Halcon, Nov. 1906 (iso-, Fl, K!, NY, P!, US).

Weinmannia camiguinensis Elmer, Leafl. Philipp. Bot. 7: 2607 (1915); Merr., Enum. Philipp. Fl. Pl. 2: 224 (1923); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930).—Type: *Elmer 14228*, Philippines, Mindanao, Island of Camiguin, Mambajao, densely wooded gulches or ravines at 3500 ft. (holo-, PNH, seen by R.D. Hoogland; iso-, A!, BM!, BO!, GH!, K!, L!, P! and numerous others cited by Bernardi).

Weinmannia bulusanensis Elmer, Leafl. Philipp. Bot. 10: 3723 (1939); nom. illeg., description in English. Collection cited: *Elmer 17293*, Philippines, Luzon, Prov. Sorsogon, Irosin (Mt. Bulusan), 1000 ft., Sep. 1916 (A!, BM!, BO!, GH!, L!, P! and others).

Weinmannia irosinensis Elmer, Leafl. Philipp. Bot. 10: 3725 (1939); nom. illeg., description in English. Collection cited: *Elmer 14918*, Philippines, Luzon, Prov. Sorsogon, Irosin (Mt. Bulusan), 1500 ft., Nov. 1915 (BM!, BO!, GH!, L!, P! and others).

Tree 7-12 m high, 12-40 cm dbh. Young stems woody, pilose, the hairs up to 0.8 mm long, older ones more sparsely pilose to glabrescent or puberulous, with minute longitudinal fissures and numerous lenticels; branching not dichotomous. Stipules caducous or not, suborbicular or reniform, up to 1.2 × 1.9 cm, base usually constricted, apex rounded, wavy or coarsely toothed, adaxial surface glabrous except at base, abaxial surface puberulous especially at base. Leaves imparipinnate with (3-)5-7(-8) pairs of lateral leaflets, total length up to 14 cm including a petiole 1.3-2.5 cm long; rachis segments 0.6-1.5 cm long; petiole and rachis segments semiterete, flattened on adaxial side, pilose and/or puberulent, often densely so on adaxial side; lateral leaflets narrowly elliptical, increasing in size distally along the rachis, the largest per leaf 2-6.5 × 0.6-1.4 cm, the base unequal, ± sessile, apex narrowly acute; apical leaflet narrowly elliptical, (2.2-)4.1-8.3 × (0.7-)0.9-2.3 cm, base shortly attenuate to petiolulate, apex narrowly acute; leaflet blades chartaceous to subcoriaceous, glabrous above, sparsely pilose below, not punctate; margin crenate to serrate, 7-11 notches on each side of the largest lateral leaflets; midrib slightly depressed above, puberulent at base, prominent below and pilose, secondary and tertiary venation slightly raised on both surfaces, reticulum not dense.

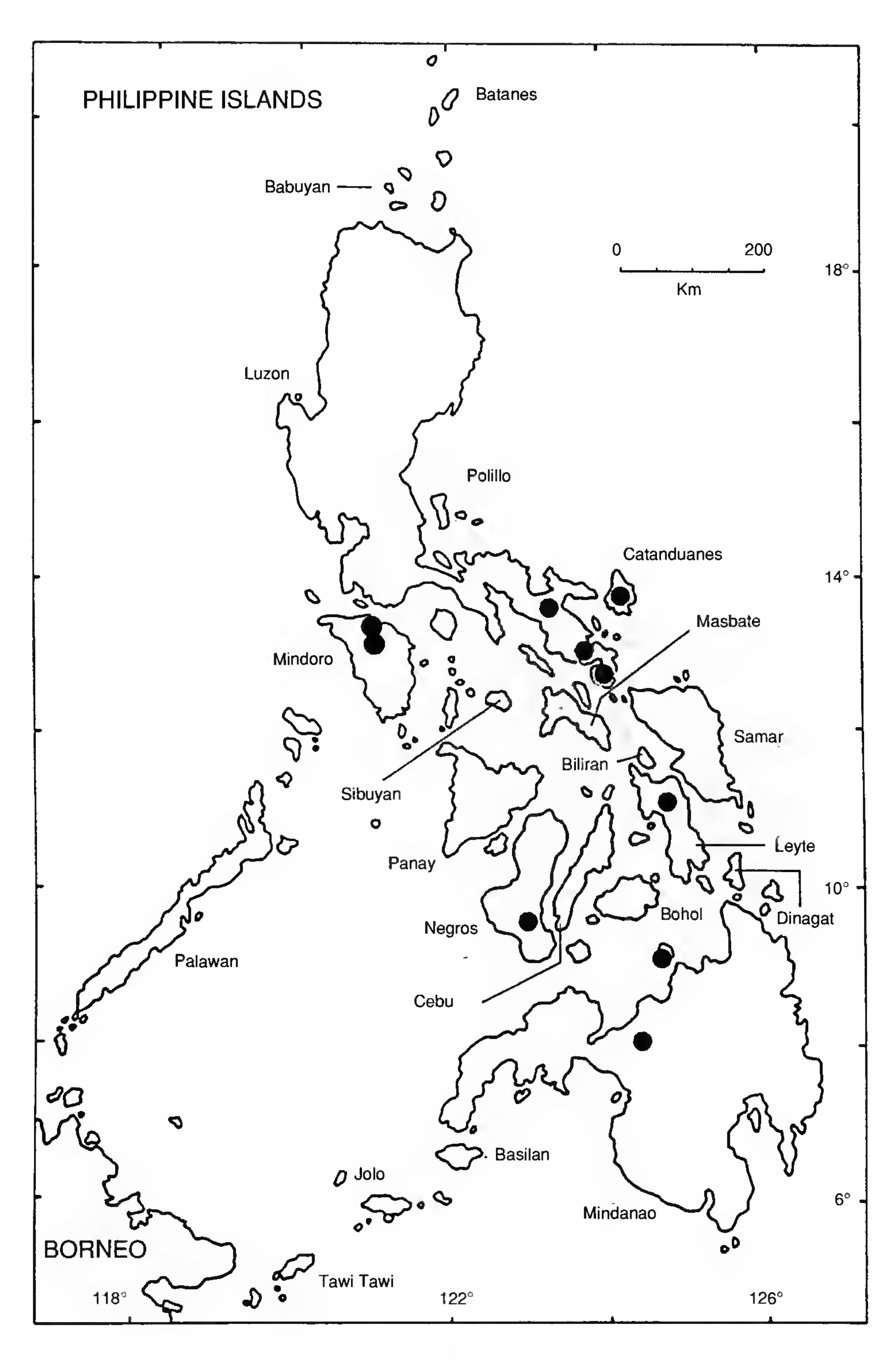


Fig. 5.—Distribution of ***Weinmannia hutchinsonii.***

Inflorescence of 1-3 pairs of dyads; sometimes a few sequential nodes producing inflorescences simultaneously; peduncles laterally flattened, 0.4-1.5 cm long, puberulous; buds at apex between the central pair of peduncles 1 or 3, sericeous; buds at apex of peduncle in angle between central pair of racemes sericeous, minute; axes of racemes densely puberulous, up to 12 cm long. Floral buds inserted in fascicles; floral bracts not seen, caducous. Flowers unisexual; pedicel 0.8-1.5 mm long, puberulous; calyx lobes 0.5-0.7 × 0.4-0.5 mm, hirsute on outer surface; corolla obovate or almost circular, 1-1.3 × 0.7-0.9 mm, rounded at apex, ciliate; disc lobes 0.2-0.3 mm long, broadly oblong; in male flowers: filaments 2.8-3 mm long, ovary 0.4 mm long, pubescent, styles 0.1 mm long, incurved; in female flowers: filaments ca. 0.9 mm long, ovary ca. 1 mm long, densely pubescent, styles ca. 0.9 mm long, straight, stigmas papillose.

Capsule 2-2.5 × 1.4-2 mm at dehiscence, the styles up to 1.5 mm long, the exocarp pubescent; calyx lobes often caducous, disc lobes persistent; central column present but shorter than valves. Seeds ca. 0.6 mm long, comose at both ends, the hairs to 1.7 mm long.—Fig. 4E-K, 5.

Breeding system.—Dioecious.

Field characters.—Bark grey-brown, vertically cracked and with ± vertical lines of corky lenticels; outer bark soft and somewhat flaky in patches, elsewhere thin and not detaching; inner bark pinkish straw; wood distinctly reddish or pinkish. Young leaves reddish. Flowers cream, light brown, whitish orange, or pinkish; immature fruit pinkish red or violet.

Distribution and ecology.—Philippines: Luzon, Catanduanes, Leyte, Negros and Mindanao. In forest on ridges and slopes, including open, disturbed areas from 325-1150 m; common (*Mendoza PNH 18409*).

Material examined.—Luzon: *Edaño BS 76206*, Prov. Camarines Sur, Mt. Isarog, Dec. 1928 (K); *Edaño PNH 34508*, Albay Prov., Mt. Malinao, fr., 3 Feb. 1956 (A, BM, K, KEP, L); *Elmer 17293*, Prov. of Sorsogon, Irosin, Mt. Bulusan, fl., Sep. 1916 (A, BM, BO, GH, K, L, P); *Mendoza 1366*, *PNH 18409*, Albay Prov., Mayon Volcano, 760 m, fr., May-June 1953 (A, K, L); *Ramos BS 23494*, Prov. of Sorsogon, yfr., July-Aug. 1915 (A, BISH, BM, BO, GH, K, L, SING); *Ramos BS 23695*, Prov. of Sorsogon, Bulusan Volcano, fr., Sep. 1915 (BM, K, P); *Sulit PNH 2717*, Sorsogon Prov., Mt. Bulusan, 380 m, fl., yfr., July-Aug. 1947 (A, BO, K, L, SING); *Sulit PNH 2781*, ibid., 390 m, yfr., July-Aug. 1947 (A, BO, L, SING); *Vidal 2717*, Prov. Camarines, Mt. Isarog, fr., Mar. 1886 (A, K).—Catanduanes: *Ramos BS 30537*, yfr., 14 Nov-11 Dec. 1917 (A, K).—Mindoro: *Coode 5393*, N coast, Subaan R. inland from San Teodoro, 450 m, yfr., 18 Apr. 1986 (A, K, L).—Negros: *Edaño PNH 6811*, Oriental, Inalacan R., W of Tanjay, 500 m, fr., Sep. 1948 (A, BO, SING).—Leyte: *Wenzel 997*, fl., 19 Aug. 1914 (GH); *Wenzel 1088*, fl., 1 Oct. 1914 (A, BM, GH).—Mindanao: *M.S. Clemens 519*, Camp Keithley, Lake Lanao, fl., May 1906 (BO, K, P).

Local names.—Torog-torig (dialect Bic); Payvagra (dialect Bir).

Weinmannia celebica may be close to this species but better collections of the former are needed to determine whether they are distinct.

2. **Weinmannia luzoniensis** S. Vidal

Revis. Pl. Vasc. Filip.: 125 (1886); Merr., Enum. Philipp. Fl. Pl. 2: 225 (1923); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Bernardi, Bot. Jahrb. Syst. 83: 172 (1964).—Type: *Vidal y Soler 314*, Philippines, Prov. Tayabas, Lucban (lecto-, here designated, MA, photo at P!; isolecto-, A!, FI, L!, MA [photos at P!]).

Weinmannia luzoniensis S. Vidal var. *puberula* Elmer, Leafl. Philipp. Bot. 8: 3078 (1919).—Type: *Elmer 18066*, Philippines, Prov. Laguna, Luzon, Mt. Maquiling, Los Banos, June-July 1917 (holo-, PNH, seen by R.D. Hoogland; iso-, A, BM!, BO!, K!, L!, P! and others).

Tree 8-20 m high, 10-50 cm dbh. Young woody stems pilose, the hairs up to 0.8 mm long, older ones more sparsely pilose to glabrescent or puberulous, with minute longitudinal fissures and numerous lenticels; branching not dichotomous. Stipules caducous or not, suborbicular, up to 1.7 × 2.2 cm, base constricted, apex rounded, both surfaces puberulous especially towards the base. Leaves imparipinnate, with 2-3(-4) pairs of lateral leaflets, total length up to 19 cm including petiole of 2-2.5 cm; rachis segments 0.5-1.5 cm long, petiole and rachis seg-

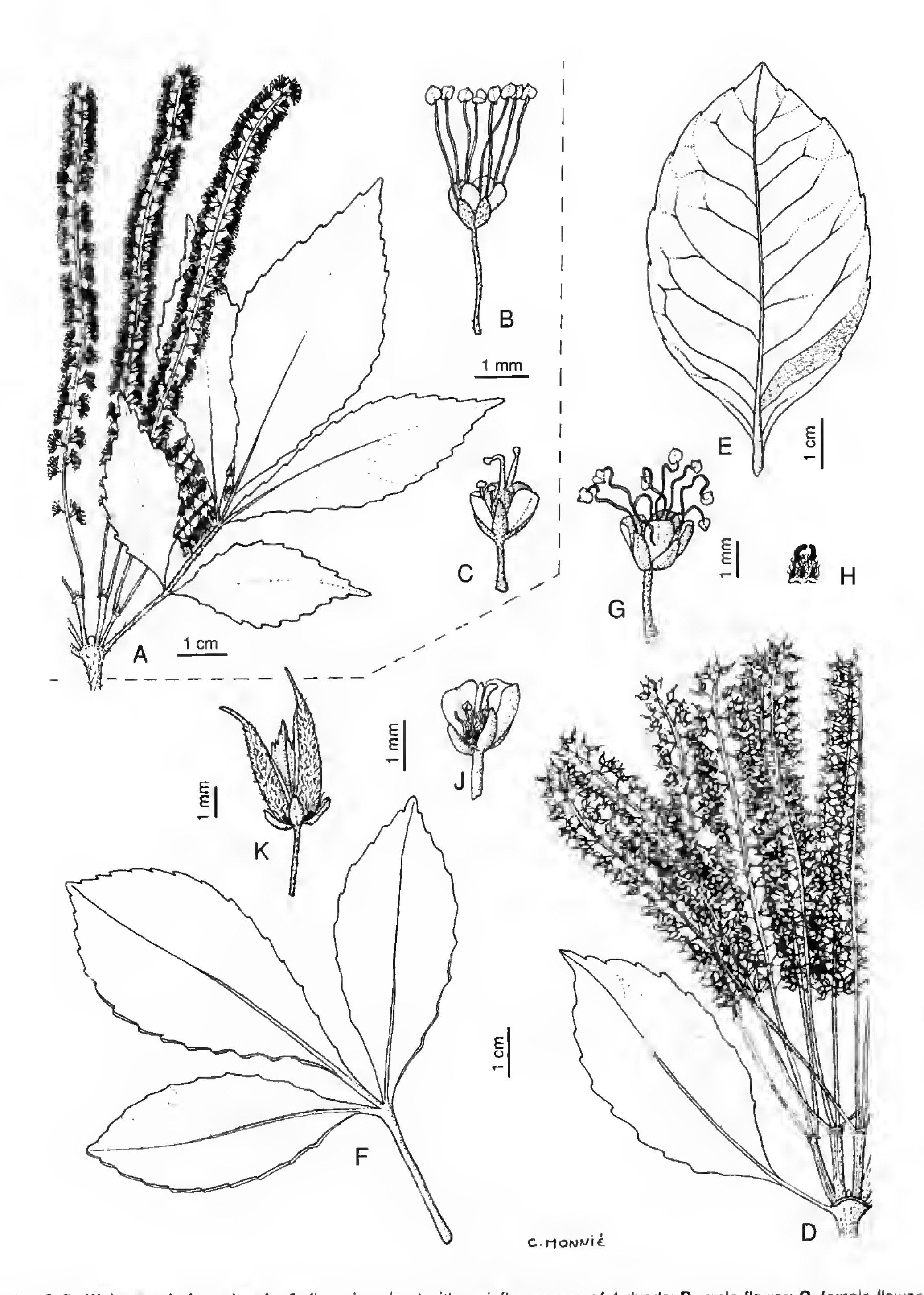


Fig. 6.—**A-C**, ***Weinmannia luzoniensis***: **A**, flowering shoot with an inflorescence of 4 dyads; **B**, male flower; **C**, female flower. (A, *Elmer 9093*; B, *Elmer 18066*; C, *Vanoverbergh 1253*).—**D-K**, ***Weinmannia negrosensis***: **D**, shoot with an infructescence of 4 tetrads; **E**, simple leaf; **F**, trifoliolate leaf; **G**, male flower; **H**, detail of G with corolla removed to show ovary, styles and disc lobes; **J**, female flower, one petal removed; **K**, capsule at dehiscence, the calyx lobes and disc lobes persistent. (D, K, *Ramos Phil. Pl. 1287*; E, G, H, *Quisumbing & Sulit BS 82442*; F, *Robinson BS 9399*; J, *Celestino PNH 7894*).—Drawn by C. MONNIÉ.

ments semiterete, flattened on adaxial side, usually somewhat pubescent or pilose at least on the adaxial side; lateral leaflets elliptical, increasing in size distally along the rachis, the largest 4.5-8.4 × 1.5-3.5 cm, the base unequal, ± sessile, apex acuminate; apical leaflet elliptical or usually markedly rhomboidal, 6.7-12 × 2.2-5 cm, base shortly attenuate to form a winged petiolule up to 1 cm long, apex acuminate; leaflet blades chartaceous to subcoriaceous, glabrous and sometimes shiny above, sparsely pilose below, not punctate; margin markedly crenate, 13-17 notches on each side of the largest lateral leaflets; midrib slightly depressed above, puberulent at base, prominent and pilose below, secondary and tertiary venation slightly raised on both surfaces, reticulum not dense.

Inflorescence usually 4 dyads or tetrads, sometimes a few successive nodes producing partial inflorescences simultaneously; peduncles laterally flattened, puberulous; buds at apex of main stem between the central pair of peduncles 1 or 3, sericeous; buds at apex of peduncle in angle between central pair of racemes sericeous, minute; axes of racemes densely puberulous, up to 9 cm long. Floral buds inserted in fascicles; floral bracts not seen, caducous. Flowers unisexual; pedicel 0.8-1.5 mm long, puberulous; calyx lobes 0.6-0.7 × 0.4-0.6 mm, hirsute on outer surface; corolla oblong or irregularly obovate, 1-1.2 × 0.6-0.8 mm, rounded or emarginate at apex, ciliate; disc lobes ca. 0.3 mm long, broadly oblong; in male flowers: filaments 2.2-3.4 mm long, ovary 0.4-0.6 mm long, pubescent, styles 0.1-0.4 mm long, incurved; in female flowers: filaments 0.7-1.2 mm long, ovary 1-1.2 mm long, densely pubescent, styles 0.9-1.1 mm long, straight, stigmas capitate, papillose.

Capsule 2-2.7 × 1.3-1.5 mm at dehiscence, the styles up to 1.5 mm long, the exocarp densely pubescent to velutinous; calyx lobes caducous or not, disc lobes persistent; central column present but shorter than valves. Seeds ca. 0.7 mm long, comose at both ends, the hairs to 1 mm long.—Fig. 6A-C, 7.

BREEDING SYSTEM.—Dioecious.

FIELD CHARACTERS.—Flowers yellowish or red (*Conklin & Buwaya PNH 80387*).

DISTRIBUTION AND ECOLOGY.—Luzon and one record from Mindanao. In mid-mountain and ridge forest, and secondary forest, from 500 to 2000 m, on clay soil. BROWN (1919) records it on Mt. Maquiling in mid-mountain forest at 700 m as amongst the more prominent first story species in the *Quercus-Neolitsea* association, and says it also occurs in dipterocarp forest and is fairly common in some localities in the mountains of Luzon.

MATERIAL EXAMINED.—**LUZON:** *Brown BS 18999*, Laguna Prov., Mt. Makiling, fl., Apr.-May 1913 (A, K); *Conklin & Rosario, PNH 72666*, Mountain Prov., Mt. Ibukakan, Banaue, buds, fl., 1 Aug. 1961 (A, K, L); *Conklin & Buwaya PNH 80387*, Mountain Prov., Bayninan, Banaue, Ifugao, 4000 ft., fl., 29 Mar. 1963 (A, K, L); *Curran FB 5070*, Benguet Prov., Baguio, fl., yfr., Aug. 1906 (BO, SING); *Elmer 8831*, ibid., fl., Mar. 1907 (A, BO, K, L); *Elmer 9093*, Prov. Tayabas, Lucaban, fl., May 1907 (A, BO, K, L); *Elmer 18024*, Prov. Laguna, Los Banos, Mt. Maquiling, fl., June-July 1917 (BM, BO, K, L, P); *Gacad FB 27274*, Benguet Subprov., Irisan, fr., May 1918 (BO, L, SING); *Hancock 82*, nr. Baguio, st., Aug. 1935 (K); *Lagasca FB 30194*, Benguet Prov., fl., July-Oct. 1925 (BO, P); *Langlassé 70*, Foot of Mt. Banajao, fr., 26 Oct. 1894 (P); *Leano FB 21846*, Benguet Subprov., fl., yfr., Jan.-May 1914 (BM, K, P); *Loher 5114*, Benguet (K); *Loher 5125*, ibid. (K); *Merrill Phil. Pl. 830*, Benguet Subprov., fl., May 1911 (K); *Merrill Phil. Pl. 1739*, Benguet Subprov., fl., May 1914 (BM, BO, GH, L, P, SING); *Meyer FB 3123*, Prov. Bataan, Lamao R., Mt. Mariveles, fl., May 1905 (K, SING); *Ramos BS 20533*, Prov. Laguna, San Antonin, fr., Feb. 1913 (BM, K, P); *Ramos BS 23673*, Prov. Sorsogon, Bulusan volcano, yfr., Sep. 1915 (K); *Sankubl 376*, Benguet Subprov., st., Feb. 1916 (A); *Sulit PNH 6989*, Laguna Prov., Mt. Makiling, Nat. Park, 500-700 m, fr., 11 Nov. 1946 (A); *Vanoverbergh 1253*, Bontoc Subprov., fl., 25 July 1914 (A, L, P); *Vidal y Soler 2002*, Benguet (K).—**MINDANAO:** *Clemens s.n.*, Camp Keithley, Lake Lanao, yfr., Sep.-Oct. 1907 (BO).

LOCAL NAMES.—Tabangawon (dialect Ifugao); Tabangawon an pahitong, Bani (Tagalog); Itangan (Igorot); Saiu (Igorot); Sayo (*Vidal y Soler 314*). Local uses: good tanbark (BROWN 1954).

TYPIFICATION.—In the protologue, VIDAL Y SOLER cites two collections, *314* Lucban, Pr. Tayabas, and *2002* Distr. Benguet. His original set of material in Manila was destroyed by fire and the remainder of his herbarium and types are

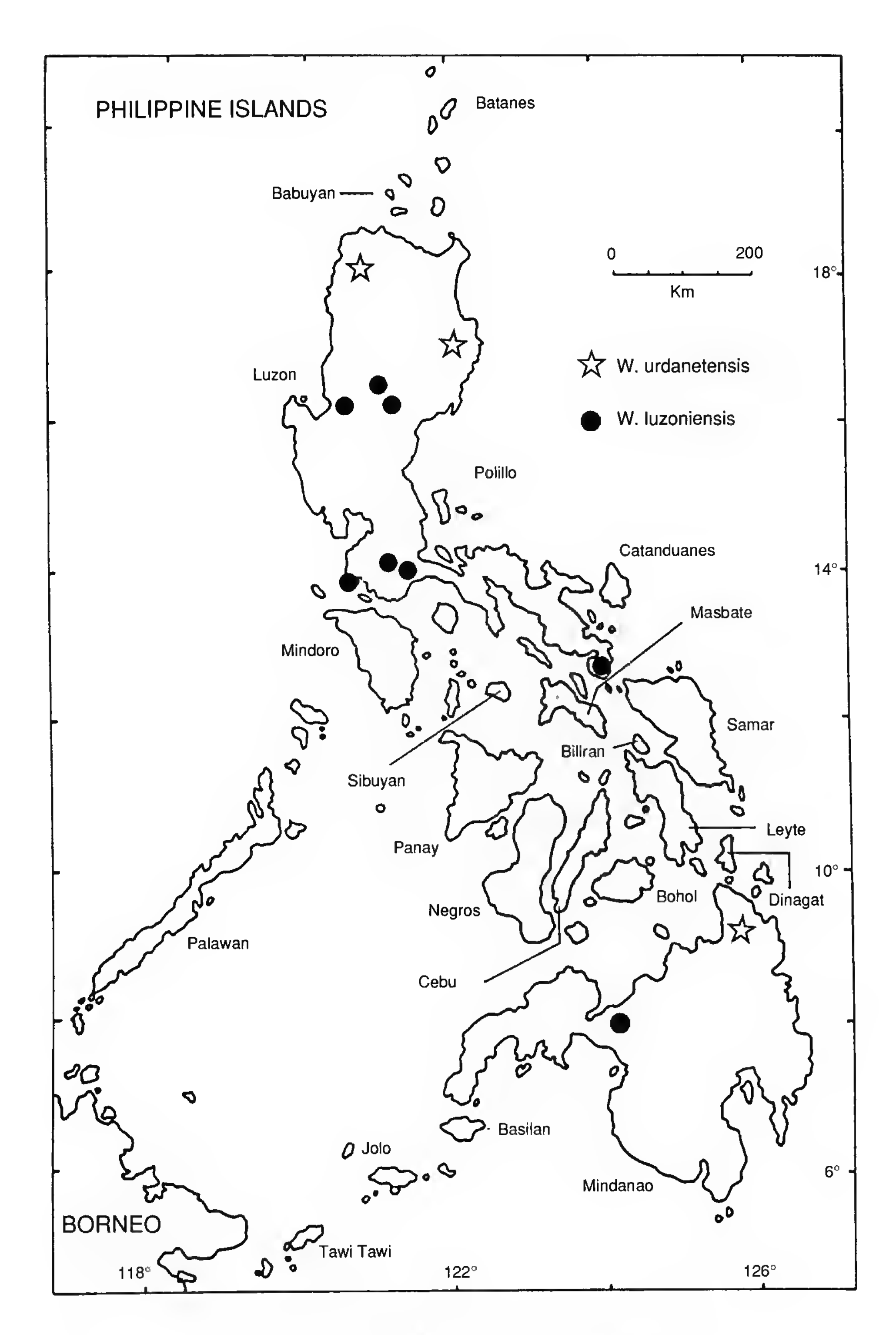


Fig. 7.—Distribution of ***Weinmannia luzoniensis*** and ***W. urdanetensis***.

at MA (STAFLEU & COWAN 1986). There are nine sheets of *314* at MA, and the one bearing a fruiting specimen and two labels with the inscription "Inspeccion Gral de Montes de Filipinas" is here designated as the lectotype.

I agree with BERNARDI (1964: 172) that var. *puberula* does not merit recognition.

3. Weinmannia negrosensis Elmer

Leafl. Philipp. Bot. 2: 577 (1909); Merr., Enum. Philipp. Fl. Pl. 2: 225 (1923); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Bernardi, Bot. Jahrb. Syst. 83: 174, t. 23 var. *negrosensis* (1964).—Type: *Elmer 9656*, Philippines, Prov. of Negros Oriental, Dumaguete, Cuernos Mts., ridge at 4250 ft., Mar. 1908 (iso-, BM!; also A, E, FI, G, LE, and Z fide BERNARDI).

Weinmannia simplicifolia Merr., Philipp. J. Sci. Bot. 12: 268 (1917); Merr., Enum. Philipp. Fl. Pl. 2: 225 (1923); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930).—*Weinmannia negrosensis* var. *simplicifolia* (Merr.) Bernardi, Bot. Jahrb. Syst. 83: 175, t. 24 (1964).—Type: *Ramos & Edaño BS 26531*, Philippines, Tayabas Prov., Mt. Dingalan, 300 m, 9 Sep. 1916 (iso-, A, K!, US).

Weinmannia cuneatifolia Engl., Nat. Pflanzenfam., ed. 2, 18a: 252 (1930).—Type: *Ramos Philipp. Pl. 1287*, Philippines, Mindanao (holo-, B, seen by R.D. HOOGLAND; iso-, BM!, L!, P! and others).

Shrub or tree 3-25 m high, up to 30 cm dbh when 12 m high. Young stems glabrous, older ones with numerous white lenticels; branching not usually dichotomous. Stipules caducous or not, suborbicular, up to 1.5 × 1.7 cm, base constricted, apex rounded, abaxial surface glabrous or shortly strigose especially towards the base, adaxial surface glabrous. Leaves simple or trifoliolate; total length up to 19 cm in trifoliolate leaves, including petiole of 1-4 cm; petiole subterete, slightly flattened or channelled on adaxial side, glabrous or puberulent; leaf(let) blades elliptical to obovate; in trifoliolate leaves, lateral leaflets 4.5-11.5 × 1.6-3.4 cm, base shortly attenuate, apex acute or acuminate; apical leaflet 6-15.5 × 2.4-6 cm, base long attenuate (constricted region up to 1.7 cm long), apex acute or acuminate; unifoliolate leaves 4.5-13 × 1.7-6.5 cm, base attenuate (constricted region 0.6-1.5 cm long); leaflet blades coriaceous, glabrous on both surfaces, not punctate below; margin sometimes minutely thickened and revolute, crenate, 11-15 crenations on each side of a leaflet; midrib sometimes slightly depressed above, prominent below, glabrous, secondary and tertiary venation flat or raised above and raised below, reticulum dense.

Inflorescence usually 4 dyads or tetrads, sometimes a few successive nodes producing partial inflorescences simultaneously; peduncles 0.3-1.3(-3) cm long, puberulent; buds at apex of main stem between central pair of peduncles 1 or 3, sericeous; buds at apex of peduncle in angle between central pair of racemes sericeous, minute; axes of racemes puberulent, up to 12 cm long. Floral buds inserted in fascicles; floral bracts ligulate, 1.5 mm long, ciliate. Flowers unisexual; pedicel 1-1.7 mm long, puberulent; calyx lobes 0.6-1 × 0.6-0.8 mm, glabrous on outer surface, ciliate; petals obovate, apex rounded, 1-1.4 × 0.7-0.9 mm, ciliate; disc lobes 0.3-0.4 mm long, broadly oblong; in male flowers: filaments 2.7-3.2 mm long, ovary ca. 0.5 mm long, pubescent, styles 0.1-0.2 mm long, incurved; in female flowers: filaments 0.9-1.7 mm long, ovary 1.1-1.4 mm long, pubescent, styles 1.3-1.9 mm long, straight, stigmas capitate, papillose.

Capsule 2-2.5 × 1.3-1.5 mm at dehiscence, the styles 1-1.5 mm, the exocarp pubescent or densely so; calyx lobes usually but not always persistent, disc lobes persistent; central column present. Seeds 0.8-0.9 mm long, comose at both ends, the hairs to ca. 1 mm long.—Fig. 6D-K, 8.

BREEDING SYSTEM.—Dioecious.

FIELD CHARACTERS.—Bark greyish or light yellow-brown; smooth or finely cracked. Inner bark red-brown; wood pale straw or "sappy" red, moderately hard, odourless. Young leaves reddish; old leaves bright red. Inflorescence axes reddish; flowers fragrant; corolla white tinged with red, filaments reddish towards the base; or flowers yellowish white.

DISTRIBUTION AND ECOLOGY.—Sulawesi (1 collection) and Philippines (Luzon, Mindoro, Sibuyan, Negros, Leyte and Mindoro). Recorded from upper montane forest and mossy forest at 1200-1960 m. In the type description, ELMER

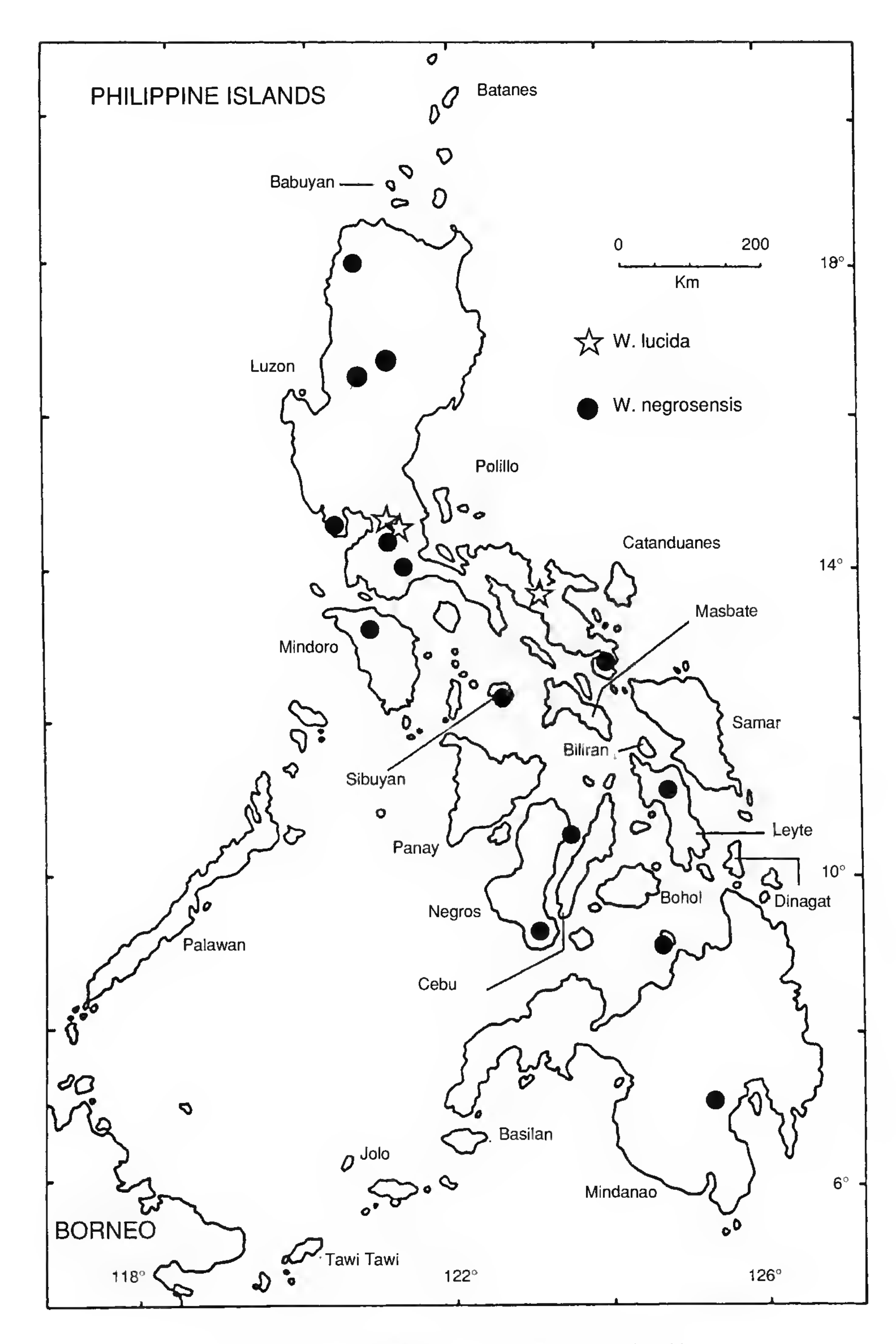


Fig. 8.—Distribution of ***Weinmannia negrosensis*** and ***W. lucida***.

records it from dense shrubberies on a windswept ridge at 4250 ft. (= 1400 m).

MATERIAL EXAMINED.—**LUZON:** *Borden FB 789*, Prov. Bataan, Lamao R., Mt. Mariveles, buds, May 1904 (BM, K); *Borden FB 1227*, ibid., fl., June 1904 (BM, K, P); *Celestino PNH 7894*, Mountain Prov., Mt. Polis, Ifugao, 2042 m?, fl., Mar. 1948 (A, L); *Loher 5989*, Rizal Prov., Montalban, fr., July 1905 (K); *Loher 5990*, Rizal, Orind?, fl., 5 Oct. 1906 (K); *Loher 12219*, Rizal Prov., fr., Dec. 1910 (A, BM, P); *Loher 12816*, ibid., fl., Mar. 1909 (BM); *Meyer FB 2756*, Prov. Bataan, Lamao R., Mt. Mariveles, fl., fr., Feb. 1904 (K); *Quisumbing & Sulit BS 82442*, Benguet Subprov., Mt. Singakalsa, Mar. 1931 (A); *Ramos BS 23500*, Prov. Sorsogon, fr., July-Aug. 1915 (A, K, P); *Ramos BS 23666*, Prov. Sorsogon, Bulusan Volcano, fl., Sep. 1915 (BM); *Ramos BS 33366*, Ilocos Norte Prov., Mt. Palimlim, fl., Aug. 1918 (A); *Robinson BS 9399*, Prov. Tayabas, Infanta, fr., Aug. 1909 (L, P); *Whitford 420*, Prov. Bataan, Lamao R., Mt. Mariveles, fl., June 1904 (K, P); *Whitford s.n.*, Prov. Bataan, Lamao R., st., May 1905 (K).—**MINDORO:** *Coode 5717*, NE Mindoro, Ramayan, Mt. Halcon complex above Paitan on Dulangan R., 1200 m, st., 8 May 1986 (L).—**SIBUYAN:** *Argent & Reynoso 89125*, Romblon Prov., above Magdiwang on ridge leading to Mayos Peak, 1350 m, fl., 27 Aug. 1989 (K).—**NEGROS:** *Edaño PNH 21958*, Negros Occidental, Mt. Canlaon, 1960 m, st., 10 Apr. 1954 (K, L).—**LEYTE:** *Wenzel 1057*, fr., 14 Aug. 1914 (A, BM).—**MINDANAO:** *Co 3135*, N Cotabato Prov., Kidapawan Muncip., Mt. Apo, NW slope, trail between Lake Ago and Apo Geothermal project site B, 1320 m, buds, 24 Oct. 1990 (A); *Ramos Phil. Pl. 1287*, Camiguin, fr., Apr. 1912 (BM, L, P).

LOCAL NAMES.—Basikong (Bagobo language); Tangolamos-itum (Visayan).

TYPIFICATION.—ENGLER did not cite a particular collection in the protologue of *Weinmannia cuneatifolia*, but only the locality, Mindanao. On the basis of this, the RAMOS collection at B is considered to be the holotype.

BERNARDI (1964) recognised two varieties which had either simple or trifoliolate leaves: var. *simplicifolia* and var. *negrosensis*. However, several specimens have both types of leaves so var. *simplicifolia* is not maintained here.

4. Weinmannia lucida Merr.

Philipp. J. Sci. Bot. 10: 7 (1915); Merr., Enum. Philipp. Fl. Pl. 2: 225 (1923); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Bernardi, Bot. Jahrb. Syst. 83: 170, t. 21 (1964).—Type: *Ramos Philipp. Pl. 1109*, Philippines, Luzon, Prov. Laguna, Dahican, in forest along river, 17 Sep. 1912 (iso-, US!; also FI, G, JE, M, U and Z, fide BERNARDI).

Shrub or small tree 3-10 m high. Young stems ± glabrous, older ones glabrous with minute longitudinal fissures; branching not dichotomous. Stipules caducous or not, suborbicular, up to 0.7 × 0.9 cm, base constricted and puberulous on abaxial surface, glabrous on adaxial side, apex rounded. Leaves imparipinnate, lateral leaflets (1-)2-3 pairs, total length up to 18 cm including petiole of 1.5-3.5 cm; rachis segments 1.2-3 cm long, petiole and rachis segments subterete, slightly flattened or channelled on adaxial side, sometimes densely puberulent; leaflets elliptical to broadly elliptical, often conduplicate when dry; lateral leaflets 5-8.5 × 2-3.7 cm, the blade narrowing unequally at the base into a petiolule ca. 0.5 cm long, apex acuminate; apical leaflet 7-9.5 × 2.5-3.5 cm, not markedly larger than the largest laterals, base attenuate to form a petiolule ca. 1 cm long, apex acuminate; leaflet blades subcoriaceous, glabrous and shiny on both sides, drying dark brown above and reddish brown below, not punctate; margin sometimes minutely revolute, crenate, 8-10 notches on each side of a leaflet; midrib slightly depressed above, prominent below, secondary and tertiary venation slightly raised on both surfaces, reticulum not dense.

Inflorescence usually 4 dyads or tetrads, sometimes a few successive nodes producing partial inflorescences simultaneously; peduncles 0.5-1 cm long, shortly puberulous; buds at apex of main stem between central pair of peduncles 1 or 3, sericeous; buds at apex of peduncle in angle between central pair of racemes sericeous, minute; rachises puberulous, up to 12 cm long. Floral buds inserted in fascicles; floral bracts caducous. Female flowers (*Sulit PNH 6329*): pedicel 3 mm long, puberulous; calyx lobes 0.6 × 0.5 mm, glabrous; corolla oblong, 1.1 × 0.8 mm; disc lobes 0.3 mm long, broadly oblong; filaments 1 mm long; ovary 1.1 mm long, densely pubescent; styles 1.4 mm long, straight; stigmas capitate, papillose.

Capsules 2.5 × 1.5 mm at dehiscence, the styles

ca. 1 mm, the exocarp densely pubescent; calyx lobes caducous, disc lobes persistent; central column present but shorter than valves. Seeds ca. 0.8 mm long, comose at both ends, the hairs to 1.5-2 mm long.—Fig. 8.

BREEDING SYSTEM.—Apparently dioecious.

DISTRIBUTION AND ECOLOGY.—Luzon and ?Samar. *Edaño BS 76049* gives "summit of forest at 2000 ft. [= 650 m], plant 3 m × 12 cm dbh, flower whitish pink". *Sulit PNH 6329* (*W.* cf. *lucida*) is from dipterocarp forest at ca. 230 m on the island of Samar and is omitted from the distribution map.

MATERIAL EXAMINED.—**LUZON**: *Edaño BS 76049*, Camarines Sur, Mt. Madooy, 2000 ft., fr., 10 Nov. 1928 (A, SING); *Loher 5991*, Montalban, Rizal, ft., 5 Nov. 1906 (BO, K); *Ramos BS 23806*, Prov. Laguna, San Antonio, yfl., Oct. 1915 (A).

***W.* cf. lucida.**— **SAMAR**: *Sulit PNH 6329*, Bagacay, Concord, 230 m, fl., Apr.-May 1948 (A, L).

This is a poorly defined species intermediate between *Weinmannia negrosensis* (from which it differs by having less coriaceous leaves, the reticulum of tertiary and quaternary venation never as strongly pronounced, and the leaves never simple) and *W. luzoniensis* (which has pilose indumentum on the stems and leaf rachises, the terminal leaflet are ± rhomboidal, and the margin is more distinctly crenate). However, field observations and better ecological information are required before *W. lucida* can either be equated with another taxon or more clearly distinguished.

5. Weinmannia urdanetensis Elmer

Leafl. Philipp. Bot. 7: 2608 (1915); Merr., Enum. Philipp. Fl. Pl. 2: 225 (1923); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); L.M. Perry, J. Arnold Arbor. 30: 160 (1949); Bernardi, Bot. Jahrb. Syst. 83: 181 (1964) excl. t. 29.—Type: *Elmer 13701*, Philippines, Mindanao, Prov. of Agusan, Cabadbaran (Mt. Urdaneta), Sep. 1912 (iso-, A, BM!, BO!, BISH!, K!, L! and others).

For synonomy, description and illustration, see New Guinea (Part 3, HOPKINS 1998b p. 74). Material from the Philippines closely resembles some collections from Irian Jaya.

DISTRIBUTION AND ECOLOGY (Fig. 7).—Philippines (Luzon and Mindanao) and New Guinea. In Philippines, known from only three collections. *Clemens 16904* describes it as a "summit tree or high shrub". In New Guinea, it grows in montane forest at 1000-3250 m, at higher altitude in the Central Highlands.

MATERIAL EXAMINED.—**LUZON**: *Clemens 16904*, Isabela Prov., Mt. Moises, st., Apr. 1926 (SING); *Ramos BS 33268*, Ilocos Norte Prov., Mt. Palimlin, yfr., Aug. 1918 (A, K, P).

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A revision of *Weinmannia* (Cunoniaceae) in Malesia and the Pacific. 3. New Guinea, Solomon Islands, Vanuatu and Fiji, with notes on the species of Samoa, Rarotonga, New Caledonia and New Zealand

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KEY WORDS
Weinmannia,
Cunoniaceae,
New Guinea,
Solomon Islands,
Vanuatu,
Fiji,
New Caledonia.

ABSTRACT
Species of *Weinmannia* belonging to two sections occur in eastern Malesia and the western Pacific: sect. *Fasciculata* is largely Malesian, extending as far east as Fiji, and sect. *Leiospermum* is largely Pacific and occurs as far west as Papua New Guinea. In total, about 20 species occur in the region from New Guinea to the Cook Islands. *Weinmannia fraxinea*, which is widespread in Malesia, also occurs in New Guinea and the Solomon Islands. *Weinmannia croftii* from Papua New Guinea (Bismarck Archipelago and Karkar Island) is described as new, and the new combination *W. ouaiemensis* is published for a species in New Caledonia. There is a high level of endemism within the various island groups of this region, although the status of species from Samoa and the Cook Islands has not been resolved. Regional keys, illustrations and distribution maps are provided.

RÉSUMÉ

Plusieurs espèces de *Weinmannia*, appartenant à deux sections, existent dans l'est de la Malésie et l'ouest du Pacifique. La sect. *Fasciculata*, en grande partie de Malésie, s'étend vers l'est jusqu'à Fidji ; la sect. *Leiospermum*, essentiellement du Pacifique se trouve vers l'ouest jusqu'à la Papouasie-Nouvelle-Guinée. Au total, environ 20 espèces se trouvent dans la région comprise entre la Nouvelle-Guinée et les Iles Cook. *Weinmannia fraxinea*, largement répandu en Malésie, existe aussi en Nouvelle-Guinée et aux Iles Salomons. *Weinmannia croftii* de Papouasie-Nouvelle-Guinée (Archipel Bismarck et Ile Karkar) est une nouvelle espèce décrite ici, et une nouvelle combinaison, *W. ouaiemensis*, est proposée pour une espèce de Nouvelle-Calédonie. Le taux d'endémisme au sein des divers groupes d'îles de cette région est très élevé, bien que le statut des espèces de Samoa et des Iles Cook n'ait pas encore été résolu. Des clés de détermination régionales, des illustrations et des cartes de distribution sont présentées.

MOTS CLÉS
Weinmannia,
Cunoniaceae,
Nouvelle-Guinée,
Iles Salomons,
Vanuatu,
Fidji,
Nouvelle-Calédonie.

INTRODUCTION

This is the third part of a revision of the Malesian-Pacific species of *Weinmannia*. Part 1 (HOPKINS 1998a) gives a general introduction, including definitions of the terms used for the structure of the inflorescence, and describes the species of western Malesia. Parts 2 and 4 (HOPKINS 1998b; HOPKINS & FLORENCE 1998) deal with the species of Sulawesi and the Philippines, and the central Pacific respectively.

The *Weinmannia* species dealt with here show considerable island or island-group endemism, although a number which occur on volcanic islands and belong to sect. *Leiospermum* appear to be closely related to one another, and the morphological differences between them are relatively small. In addition to the new species and new combination published here, incomplete material from Irian Jaya and the Solomon Islands (including Bougainville which is politically part of Papua New Guinea) appears to represent a handful of undescribed taxa.

I. WEINMANNIA IN NEW GUINEA AND THE BISMARCK ARCHIPELAGO

Four named species occur in this region, *Weinmannia fraxinea*, *W. urdanetensis*, *W. pullei* (all sect. *Fasciculata*) and *W. croftii* (sect. *Leiospermum*). *Weinmannia pullei* and *W. croftii* are endemic. Some small-leafleted collections from Irian Jaya may represent additional taxa but better collections are needed, and they are not included in the key.

Key to the species of New Guinea and the Bismarck Archipelago

1. Flowers inserted on inflorescence axes in fascicles, i.e. a group of pedicels subtended by each bract; inflorescence usually composed of 1-3 pairs of dyads or tetrads inserted in the axils of the most distal pair of leaves; apical bud of shoot, between central peduncles of the partial inflorescences, present and usually dormant 2

1'. Flowers inserted on inflorescence axes singly, i.e. each individual pedicel subtended by a bract; inflorescence usually a central triad or pentad, developing from the apical bud of the shoot .... **4. W. croftii**

2. Lateral leaflets in 1-4(-6) pairs, 3-10 × 0.8-3 cm; mature seeds comose at each end; inflorescence usually of 1-3 pairs of dyads or tetrads .... **1. W. fraxinea**

2'. Lateral leaflets in 1-19 pairs, 0.6-3.2 × 0.3-1.5 cm; mature seeds bearing hairs all over surface; inflorescence usually a pair of dyads 3

3. Lateral leaflets oblong or elliptical, 2-19 pairs; secondary veins oriented at 90° to main vein; leaflets inserted at 90° to leaf rachis, often strigose-velutinous on underside; calyx pubescent .... **3. W. urdanetensis**
3'. Lateral leaflets obovate, 1-6 pairs; secondary veins oriented at an acute angle to main vein; leaflets inserted at an acute angle to the leaf rachis, usually glabrous on underside; calyx glabrous .... **2. W. pullei**

1. Weinmannia fraxinea (D. Don) Miq.

For synonomy, description, illustration and distribution map, see part 1 (HOPKINS 1998a: 23).

BREEDING SYSTEM.—Flowers usually bisexual in New Guinea, rarely unisexual (male: *Ledermann 9922, 9784, Henty & Foreman NGF 42671*, all from West Sepik; female: *Stevens LAE 58123* and *Brass 22460*).

FIELD CHARACTERS.—Small treelet to emergent, 5-35 m, up to 70 cm dbh, trunk rarely with buttresses up to 8 m. Bark variable, pale to dark brown or grey, smooth, cracked, fissured, scaly or with pustules; inner bark brown or reddish brown; sap wood white, straw, pink-straw, sometimes turning purple, hard; heartwood pink or red; sometimes with sticky exudate. Buds and inflorescence axes pink. Flowers whitish, sometimes tinged with pink, red or green; smell fragrant or unpleasant.

DISTRIBUTION AND ECOLOGY.—Malesia (except Sulawesi and Philippines) to Solomon Islands. See HOPKINS 1998a, Fig. 8, p. 29. In New Guinea, from 10 m (Vogelkop) to 1450 m and rarely to 2250 m (Mt. Dayman, Milne Bay and Mt. Talawe, East New Britain). Found in a wide range of forest habitats including lowland rain forest, hill forest, lower montane and cloud forest up to the border of subalpine grassland on Mt. Dayman; frequently from steep slopes and ridge tops; in primary forest, disturbed forest and regrowth and described as characteristic of older second growth at 350 m; scattered to dominant. Juvenile plants common on road cuts and open areas (Morobe, 100-150 m).

At low altitude (< 200 m), associates include Linaceae and *Anisoptera*. At mid elevation (300-950 m) found in hill forest with *Castanopsis*, *Agathis*, *Freycinetia*, and *Pandanus*; also in hill forest on limestone karst (600 m, New Ireland), lower montane, moderately dry forest dominated by *Eucalyptopsis* (450 m, Normanby Island), and lower montane forest dominated by *Weinmannia* and *Alstonia spectabilis* (950 m, New Ireland). At higher elevations grows with *Podocarpus* and *Dacrydium*.

Weinmannia fraxinea is frequently recorded from lower elevation in New Guinea and the Solomons than for instance in Java, Sumatra and the Malay Peninsula though usually from the same types of habitat (e.g. road cuts and open areas, hill forest and lower montane forest).

SELECTED COLLECTIONS (from a total of 63 studied for this region).—**IRIAN JAYA:** *Aet & Idjan 806*, Memperawaja nr. Seroei, buds, 16 Sep. 1939 (A, BO, K, L, SING); *Dijk bb 30351*, Ond. afd. Seroei, Eil. Japen, 800 m, st., 3 Aug. 1939 (A, BO, L); *Kanehira & Hatusima 12797*, Boemi, 40 km inward of Nabire, 300 m, buds, fr., 11 May 1940 (BO, L, type of *W. hypoglauca*); *Koster BW 8112*, Div. Hollandia, Bodem R., 60 km SE from Sarmi, 70 m, buds, 10 Feb. 1959 (A, L); *Lam 1574*, R. Mamberamo, nr. Mt. Doorman, 1450 m, fl., 9 Oct. 1920 (BO, K); *Schram BW 6009*, Vogelkop, Beriat, ± 20 km S of Teminaboean, 10 m, st., 19 Apr. 1958 (L); *Sijde BW 4071*, Hollandia, Cycloop Mts., Bivouac 1, 500 m, yfr., 12 Sep. 1956 (A, K, KEP, L); *Soengeng Reksodihardjo 386*, SE West Irian, Ingembit to Opka, fr., 8 June 1967 (L); *Vink BW 8426*, Div. Hollandia, Sidoarsi Mts., ca. 200 km W of Hollandia, 200 m, st., juv., 20 May 1959 (L).—**PAPUA NEW GUINEA:** ***Western***: *Henty et al. NGF 31797*, nr. Ingembit village, 480 ft., fr., 8 June 1967 (BISH, K, L); *Ridsdale & Galore NGF 33436*, Kiunga, 200 ft., fl., 21 July 1967 (A, K, L). ***West Sepik***: *Darbyshire 258*, nr. Miwaute village, Torricelli Mts., Lumi subdistr., 2600 ft., fl., 23 Aug. 1961 (A, BISH, CANB, K, L); *Darbyshire & Hoogland 8374*, nr. Wantipi village on Bliri R., Aitape subdistr., 800 ft., fl., 3 Aug. 1961 (A, BISH, BM, CANB, K, L); *Henty & Foreman NGF 42671*, Kokomo Creek, trib. of Frieda R., Telefomin subdistr., 2300 ft., fl., 28 June 1969 (A, BISH, K, L); *Ledermann 10129*, Lordberg, 1000 m, fr., 6 Dec. 1912 (K, type *W. alta*). ***East Sepik***: *Ledermann 8172*, Hunstein Mts., 2-300 m, fr., 9 Aug. 1912 (B, type *W. tomentella*). ***Madang***: *Pullen 1040*, between Aiome Patrol Post and Togum village, 1000 ft., fl., 23 Aug. 1958 (A, BM, CANB, K, L). ***Morobe***: *Clemens 1407*, Wareo, 2000 ft., yfr., 28 Dec. 1935 (A, L); *Croft & Lelean LAE 68552*, Natter Bay logging area, 93 km SE of Lae, 100 m, 30 July 1976 (A, K, L); *Croft et al. LAE 68601*, track from Tigedu to Sambiang, E of

Mongi R., 25 km E of Finschhafen, 800 m, fr., 17 Sep. 1976 (A, BISH, BM, K, L); *Hartley 12829*, above Bakaia, ca. 15 miles SE Garaina, 3000 ft., fl., 26 Jan. 1964 (A, L, P); *Takeuchi 7135*, Markham village along margin of Labu swamp, 100-150 m, fr., 4 July 1991 (A, L); *Streimann NGF 26111*, Tiaura, Kipu, 2600 ft., fl., 7 Jan. 1966 (A, K, L); *Womersley NGF 19044*, Oomsis logging area, 1800 ft., buds, yfr., 29 Nov. 1963 (A, BISH, K, L). ***Oro***: *Pullen 5931*, N side of Sibium Range, S of Toma, Bariji-Managalasa, 3500 ft., st., 9 Sep. 1964 (L). ***Milne Bay***: *Brass 22460*, N slopes Mt. Dayman, Maneau Range, 2250 m, fr., 24 May 1953 (A, L); *Smith NGF 1355*, nr. Mapo, 1100 ft., fr., Mar. 1945 (A, BISH, K, L); *Stevens LAE 58123*, Mt. Duau, above Agaun, 1460 m, fl., 1 Feb. 1973 (A, K, L); *Croft LAE 71111*, Normanby Island, NE of Bwasiaiai, 450 m, fl., fr., 2 Dec. 1977 (A, BISH, K, L); *Croft et al. LAE 68620*, S Fergusson Island, track between Ailuluai and Agamoia, 720 m, fr., 3 Nov. 1976 (A, BISH, K, L); *Brass 27428*, Misima Island, Mt. Sisa, N slopes, 350 m, fl., fr., 20 July 1956 (A, K, L); *Gideon LAE 73267*, Tagula Island, Mt. Riu, 600 m, fr., 11 Mar. 1979 (BISH, K, L). ***New Britain***: *Frodin NGF 26807*, Mt. Talawe, Talasea, 6400 ft., fr., 25 May 1966 (A, BISH, BM, CANB); *Isles et al. NGF 34400*, 6 miles E of Fullerborn Harbour, 300 m, fr., 8 May 1973 (A, BISH, K, L); *Sayers NGF 21989*, Pirilongi village, Kandrian subdistr., 1300 ft., fr., 14 Mar. 1965 (L). ***New Ireland***: *Croft LAE 65576*, 5 km S of Logagon village, N Schleinitz Range, Logagon subdistr., 600 m, fr., 23 Oct. 1974 (A, BISH, BM, L); *Gideon LAE 77167*, Lelet farm, Lelet Plateau, Konos subprov., 950 m, fr., 29 Oct. 1984 (A, K, L).

LOCAL NAMES.—Mesjeforon (Tehid language, Vogelkop); Saboo (Tor language) and Hassip (Manikiong language) both from Sidoarsi Mts.; Tima (Orne language, Wantipi) and Yeh-peh (Wapi language, Miwaute) both W Sepik; Yibit(s) (Western Prov.); Suweti (middle Waria, Morobe); Gabisamina (Upper Waria, Milne Bay); Vani'Idaidalava (Fergusson Island).

VARIATION AND RELATIONSHIPS.—A complex and variable ochlospecies, and several names from New Guinea have been put into synonomy for the first time (see HOPKINS 1998a, p. 23). Relatively variable within New Guinea, showing almost the complete range of variation on this one island. There is no morphological overlap with *Weinmannia pullei* and *W. urdanetensis* even though the largest leaflets of *W. pullei* may approach the size of the smallest ones in *W. fraxinea*.

2. Weinmannia pullei Schltr.

Bot. Jahrb. Syst. 52: 164 (1914); Nova Guinea 12: 492, t. 192 (1917); Engl., Nat. Pflanzenfam., ed. 2, 18a: 255 (1930); Bernardi, Bot. Jahrb. Syst. 83: 176, t. 25 (1964); P. Royen, Alpine Fl. New Guinea 4: 2539, t. 739 (1983).—Type: *Pulle 470*, West New Guinea (Irian Jaya), on summit of Mt. Perameles, ca. 1100 m, 27 Nov. 1912 (holo-, B; iso-, BM!, BO!, K!, L!).

Weinmannia virgulata Schltr., Bot. Jahrb. Syst. 52: 164 (1914); Nova Guinea 12: 492 (1917); Engl., Nat. Pflanzenfam. ed. 2, 18a: 255 (1930).—Type: *Pulle 692*, West New Guinea (Irian Jaya), on Mt. Hellwig, ca. 1700 m, 15 Dec. 1912 (holo-, B; iso-, BO!, L!).

Weinmannia versteeghii L.M. Perry, J. Arnold. Arbor. 30: 162 (1949); Bernardi, Bot. Jahrb. Syst. 83: 183 (1964).—Type: *Brass & Versteegh 10469* (Irian Jaya), 9 km north-east of Lake Habbema, 2700 m, Oct. 1938 (holo-, A; iso-, BM!, BO!, K!, L!).

Shrub or tree (1.75-)4-27 m high, up to 30 cm dbh, rarely epiphytic. Young stems, buds and young leaves sericeous, older stems glabrescent, bearing numerous pale lenticels. Branching not usually dichotomous. Stipules usually caducous, ligulate to ± orbicular or reniform, up to 0.8 × 1 cm, narrowing at base, apex rounded, abaxial surface strigose especially towards the base, adaxial surface glabrous. Leaves imparipinnate with 1-6(-10) pairs of lateral leaflets, total length up to 10.5 cm long, including petiole 0.7-1 cm long; rachis segments ca. 0.8 cm long; petiole and rachis diverging from the stem at an acute acroscopic angle, terete or somewhat flattened on upper surface just below point of insertion of leaflets, sometimes winged, the wings extending to 0.8 mm on either side of mid line, petiole and rachis glabrous, or puberulous above, or tomentose, the hairs up to 0.5 mm long; lateral leaflets obovate or oblanceolate, 0.6-3.2 × 0.3-1.5 cm, inserted at an acute acroscopic angle to the leaf rachis, base equal, apex acute to obtuse; terminal leaflet narrowly elliptical to elliptical, 0.8-4.8 × 0.3-1.7 cm, base attenuate, apex acute; blade flat above, usually glabrous on both surfaces, sometimes sparsely strigose below especially on midrib, subcoriaceous, not punctate; margin crenulate or rarely dentate with 3-7 notches on each side in the lateral leaflets; on upper surface, midrib and secondary veins ± flat, secondary

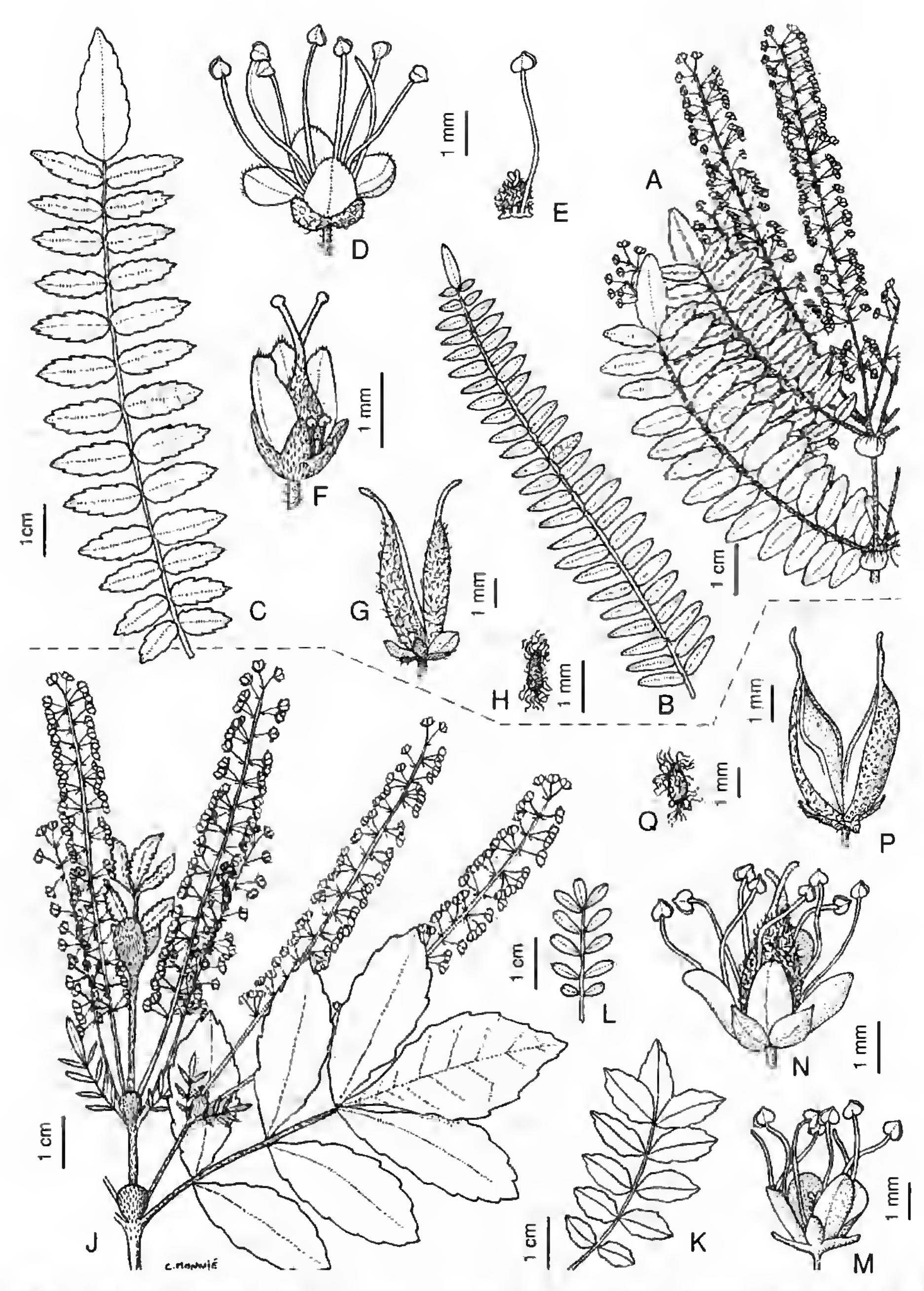


Fig. 1.—**A-H**, ***Weinmannia urdanetensis***: **A**, flowering shoot with inflorescence consisting of a dyad (base only) and a tetrad; **B**, **C**, leaves showing range in leaflet shape and number; **D**, male flower; **E**, detail of D with perianth removed to show pubescent gynoecium with short styles, minute disc lobes and a single stamen; **F**, female flower with one petal removed to show short filaments; **G**, capsule at dehiscence with persistent calyx and one petal remaining; **H**, seed. (A, *Bowers 401*; B, *Versteegh BW 10312*; C, *Robbins 2922*; D, E, *Hoogland & Pullen 5463*; F, *Wade ANU 7663*; G, H, *Paijmans 1315*).—**J-Q**, ***Weinmannia pullei***: **J**, flowering shoot with an inflorescence consisting of four racemes subtended by a pair of reduced leaves, the apical bud between the dyads continuing to grow vegetatively, and another pair of racemes borne on a lateral shoot, also subtended by reduced leaves; **K**, **L**, leaves showing range in leaflet size and shape; **M**, male flower; **N**, bisexual flower; **P**, capsule at dehiscence with persistent calyx; **Q**, seed. (J, *Hoogland & Schodde 6979*; K, M, *Vink 17098*; L, *Vinas & Wiakabu LAE 59405*; N, *Womersley NGF 24540*; P, Q, *Hoogland & Schodde 7685*).—Drawn by C. MONNIÉ.

veins at an acute acroscopic angle to the main vein; midrib prominent below.

Inflorescence usually of 2 dyads, the apical bud of main stem sometimes aborting or continuing to grow vegetatively during flowering, or rarely of 2 or 4 individual racemes; sometimes a few successive nodes producing dyads simultaneously; a pair of reduced leaves and a pair of stipules usually present at base of the racemes in each dyad; peduncles 0.6-2 cm long; racemes up to 12 cm long; buds at apex of peduncles between bases of racemes minute, velutinous, sometimes starting to grow during reproduction; peduncles and rachises usually sparsely puberulent. Floral buds inserted in fascicles, floral bracts elliptical, often hairy, 1-1.2 × 0.5 mm, persistent; flowers mostly unisexual, sometimes bisexual; pedicel 1.5-3.5 mm long, puberulent or ± glabrous; calyx lobes ca. 0.5 × 0.4-1.4 × 1.1 mm, glabrous or with ciliate margin; petals elliptic, 1.1-2.3 × 0.7-1.5 mm, margin minutely ciliolate; disc lobes 0.3-0.6 mm long; in male flowers: filaments up to 4.1 mm long, ovary 0.5-1 mm, pubescent, styles 0.2 mm long, incurved; in female flowers: filaments up to ca. 0.8 mm long, ovary 0.5-1 mm long, pubescent, styles ca. 0.9 mm long, straight, puberulent at least at base, stigmas capitate, papillose; in bisexual flowers: filaments ca. 4 mm long, ovary ca. 1 mm long, styles ca. 1 mm long, straight.

Capsules 3-4.5 × 2.5-2.8 mm at dehiscence, the styles 0.7-1.2 mm long, the exocarp densely pubescent; calyx lobes persistent; central column about half length of valves. Seeds ca. 1 mm long, bearing hairs all over surface, longest at ends.—Fig. 1J-Q, 2.

Breeding system.—Polygamodioecious? Fruits develop from flowers with both long and short filaments.

Field characters.—Outerbark brown, dark grey or cream, rather smooth with irregular

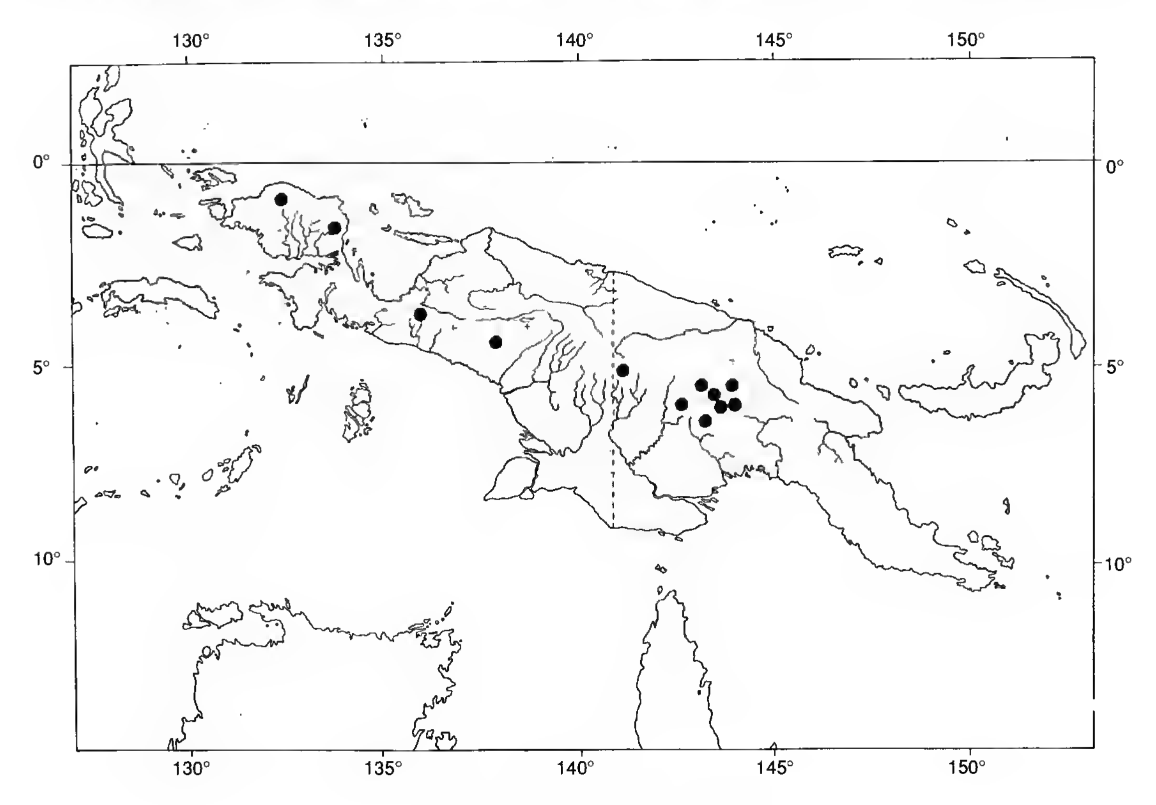


Fig. 2.—Distribution of ***Weinmannia pullei***.

cracks and lenticels; inner bark brownish, orange-brown or reddish brown. Wood cream to pink, of medium hardness, homogeneous. Flower buds light green; flowers creamy white, fragrant: sepals yellowish-green or red; corolla and filaments white; anthers pinkish-yellow; ovary light green turning pink, style pink at base and white at tip.

DISTRIBUTION AND ECOLOGY.—Endemic to New Guinea. Grows as a tree in montane forest with *Nothofagus*, *Podocarpus*, *Phyllocladus* and *Pandanus* and as a small tree or shrub in mountain top shrubbery; from 1100-2100 m in Irian Jaya and 2800-3200 m in Papua New Guinea (PNG). Common.

SELECTED COLLECTIONS (from a total of 28 studied).—**IRIAN JAYA**: *Eyma 5207*, Wissel Lakes region, Moetaro, fl., 9 Sep. 1939 (BO, L); *Eyma 5224*, ibid., Tarapadimi, S of Lake Tage Moetaro, buds, 1 Sep. 1939 (L, SING); *Pulle 488*, Mt. Perameles, 1100 m, fl., 28 Nov. 1912 (K, L).—**PAPUA NEW GUINEA**: ***West Sepik***: *Vinas & Wiakabu LAE 59405*, Telefomin subdistr., Silinmogu, ridge below Tamanagabip on track to Busilmin, 5°00'S-141°05'E, 2800 m, st., 1975 (A, BISH, K, L). ***Southern Highlands***: *Frodin NGF 26964*, N slope Mt. Ne, 9200 ft., 26 July 1966 (A, BISH, K, L); *Frodin NGF 28131*, nr. Lei camp on tack to Mt. Ambua, Tari, 8600 ft., fr., 29 July 1966 (A, L); *Gillison NGF 25132*, Ibiwara, Tari Gap, 8400 ft., 11 June 1966 (A, BISH, K, L); *Kalkman 4860*, Mt. Ne, Tari subdistr., 3140 m, 12 July 1966 (A, BISH, L); *Vink 17098*, Tari subdistr., N slope of Mt. Kerewa, 3015 m, 7 July 1966 (A, BISH, L, P). ***Enga***: *Hoogland & Schodde 6979*, nr. Poio village, SE ridge of Yaki valley, Wabag subdistr., 9000 ft., 8 July 1960 (A, BISH, BO, K, L); *Hoogland & Schodde 7685*, Yobobos grassland area, source of Lagaip R., Laiagam subdistr., 8500 ft., fr., 5 Sep. 1960 (A, BM, CANB, L); *Robbins 3056*, S slopes Ambum-Marimuni Divide nr. Londau village, Wabag area, 8000 ft., fl., fr., 24 July 1960 (CANB, L); *Womersley NGF 24540*, Kandep-Lagaip Divide, Laiagam subdistr., 9600 ft., 1 May 1965 (A, BISH, CANB, K). ***Western Highlands***: *Pullen 116*, E rim of Mt. Oga, 12 miles E of Mt. Hagen station, 8500 ft., 12 July 1957 (A, BM, K, L); *Robbins 1138*, Minj subdistr., Pinj R. valley nr. Banz R.C. sawmill, 8000 ft., st., 30 July 1957 (CANB); *Veldkamp & Stevens 5493*, Klangan Hill, S of Tomba, 2700 m, fl., 29 May 1972 (BISH, L); *Pullen 5173*, WHP/Simbu, Minj-Nona Divide, N side of Kubor Range S of Minj, 9540 ft., fl., fr., 20 Aug. 1963 (A, CANB, K, L, P).

LOCAL NAMES.—Enga language: Kain, Kain-taggan-taggan (Poio), Tagantagan and Tagar (Kepilam); Autiggli, Tewara no. 2 and Mabi (near Tari); Tandan (Mendi), Kwirap (Minj), Gubidigili (Margarima).

VARIATION.—Material of *Weinmannia* from montane New Guinea with small leaflets can be divided into two main groups, *W. pullei* (including *W. versteeghii* with a narrowly winged rachis) and *W. urdanetensis*. *Weinmannia pullei* has rather few, obovate leaflets and *W. urdanetensis* usually has more numerous elliptical or oblong ones and their leaflets also differ in their angle of insertion. These two species appear to be closely related and share the following characters: inflorescence primarily of dyads; floral bracts often persisting to fruiting stage; flowers usually unisexual but sometimes bisexual; fruits with the valves densely pubescent; seeds with hairs all over their surface and not confined only to the ends. Their distributions are largely sympatric but there is only a small minority of intermediate collections. The structure of the inflorescence is particularly variable in *W. pullei*.

Most collections of *W. pullei* are from Papua New Guinea and are relatively uniform in leaflet size, shape and vestiture, although *Vinas & Wiakabu NGF 59405* (Snow Mts., West Sepik Prov., Fig. 1L) has unusually small leaflets. Collections from Irian Jaya are more variable:
a) The three collections from near Lorentz River (Mts. Perameles and Hellwig) (*Pulle 488*, *470*, *692*) have 3-9 pairs of leaflets per leaf and the leaflets margins are dentate not crenate in two of them.
b) In the Wissel Lakes region, *Eyma 5207* is vegetatively quite close to many collections from PNG but *Eyma 5224* has trifoliolate leaves with small leaflets that are distinctly hairy on the lower surface, especially on the main vein.
c) In the Vogelkop, *van Royen & Sleumer 7224* and *Gjellerup 1159* both have largely trifoliolate leaves (the number of leaflets varies from 1-4). In the former, the leaflets are rather rounded at the apex and not very distinctly crenate; both collections are from small shrubs at 2080-2100 m.

Weinmannia versteeghii was distinguished by both PERRY (1949) and BERNARDI (1964) by its winged rachis and petiole. However, there is a continuum in the shape of the rachis and petiole within *W. pullei.*

3. Weinmannia urdanetensis Elmer

Leafl. Philipp. Bot. 7: 2608 (1915); Merr., Enum. Philipp. Fl. Pl. 2: 225 (1923); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); L.M. Perry, J. Arnold Arbor. 30: 160 (1949); Bernardi, Bot. Jahrb. Syst. 83: 181 (1964) excl. t. 29.—Type: *Elmer 13701*, Philippines, Mindanao, Prov. of Agusan, Cabadbaran (Mt. Urdanera), Sep. 1912 (iso-, A, BM!, BO!, BISH!, K!, L! and others).

Weinmannia trichophora L.M. Perry, J. Arnold Arbor. 30: 161 (1949); Bernardi, Bot. Jahrb. Syst. 83: 181 (1964).—Type: *M.S. Clemens 9498*, NE New Guinea (Papua New Guinea), Morobe Distr., nr. Samanzing, 2100-2400 m, in mountain bush, 18 Jan. 1939 (holo-, A!; iso-, B).

Weinmannia novoguineensis L.M. Perry, J. Arnold Arbor. 30: 161 (1949).—Type: *M.S. Clemens 7517*, NE New Guinea (Papua New Guinea), Morobe Distr., Sarawaket, 1800-2400 m, in mountain forest, 9 Nov. 1937 (holo-, A!; iso-, B).

Shrub or tree, 3-26 m high, up to 43 cm dbh, variable in form from bushy to gnarled to slender. Young stems velutinous, axillary buds and young leaves sericeous, older stems glabrescent, bearing numerous pale lenticels. Branching not usually dichotomous. Stipules usually caducous, ± orbicular or reniform, up to 0.8 × 1.1 cm, narrowing at base, apex rounded, abaxial surface sparsely to densely strigose especially towards the base, adaxial surface glabrous or puberulent. Leaves imparipinnate with 2-19 pairs of lateral leaflets, total length up to 10.5 cm long, including petiole ca. 0.5 cm long; rachis segments 0.3-1 cm long; petiole and rachis diverging from the stem at an angle of almost 90° especially at growing tips; petiole and rachis segments terete, densely velutinous, the hairs erect, up to 0.5 mm long; lateral leaflets elliptical, oblong or somewhat ovate, the margins ± parallel, 0.6-2.6 × 0.3-1.1 cm, inserted ± at 90° to leaf rachis, base equal or unequal, cuneate to square to cordate, apex broadly acute; terminal leaflet narrowly elliptical to elliptical, 0.9-3 × 0.3-1.2 cm, base petiolulate, the petiolule ca. 0.3 cm long, apex acute; leaflets imbricate or not, flat or revolute, usually glabrous or puberulent on upper surface, the cuticle thick and shiny, sparsely to densely strigose-velutinous below, the midrib velutinous; blades coriaceous, not punctate; margin crenulate with 4-7 notches on each side in the lateral leaflets; on upper surface, midrib and secondary veins depressed into cuticle, secondary veins ± at 90° to main vein, tertiary venation obscure, midrib prominent below.

Inflorescence a pair of dyads (rarely a pair of tetrads or 4 dyads or 4 individual racemes), sometimes a few successive nodes producing dyads simultaneously; the apical bud of the main stem between the bases of the dyads densely velutinous and often continuing to grow vegetatively during flowering; bud at apex of peduncles between bases of racemes minute, velutinous; peduncles 0.3-0.4 cm long; racemes up to 9 cm long; peduncles and axes of the racemes densely velutinous. Flowers inserted in fascicles; floral bracts elliptical, often hairy, 1.1-2 mm long, persistent; flowers unisexual or rarely bisexual; pedicel 0.5-1 mm long, puberulent or ± glabrous; calyx lobes 0.7-1 × 0.6-0.9 mm, hirsute; petals elliptical, oblong or almost circular, 1-1.9 × 0.7-1.2 mm, rounded or notched at apex, margin minutely ciliolate; disc lobes 0.3-0.6 mm long; in male flowers: filaments 2.2-3.6 mm long, ovary ca. 0.6-1 mm, pubescent, styles 0.2-0.5 mm, incurved; in female flowers: filaments 0.8-1.7 mm long, ovary 1-1.5 mm long, pubescent, styles 0.5-1 mm long, straight, puberulent at least at base, stigmas capitate, papillose; in bisexual flowers: filaments 2.6+ mm long, ovary 1-1.5 mm long, styles 1-1.8 mm long, straight.

Capsules 2.5-4 × 1.5-2 mm at dehiscence, the styles ca. 1 mm long, the exocarp densely pubescent; calyx lobes persistent; central column about half length of valves. Seeds ca. 1 mm long, bearing hairs all over surface, longest at ends.—Fig. 1A-H, 3.

BREEDING SYSTEM.—Largely dioecious but some exceptions. *Wade ANU 7663* has both male and female flowers on the same sheet (though not the same stem) and *Womersley NGF 15240* has male, female and bisexual flowers. *Robbins*

191 has male and bisexual flowers in the same inflorescence.

FIELD CHARACTERS.—Outer bark grey-brown, silver-grey or rarely black; inner bark pinkish brown with fine red streaks or dark straw brown; sap wood white to pink, pale brown or orange, very hard; heart wood pink or dark red. Floral buds green, pink or red; flowers white or cream, rarely light green.

DISTRIBUTION AND ECOLOGY.—Philippines and New Guinea. In lower montane and montane forest; also secondary forest and open scrub on limestone; often recorded from ridges or on steep slopes; abundant and gregarious. Associates include *Litsea*, *Pandanus*, *Cinnamomum* and *Nothofagus*. In the Central Highlands of Papua New Guinea, recorded from 2500-3250 m but at lower elevations elsewhere (e.g. 1000-1900 m in Irian Jaya, 1200 m in Torricelli Mts., 1500 m in Hunstein Mts. and 1770 m on Mt. Simpson, Milne Bay Prov.).

SELECTED COLLECTIONS (from a total of 47 studied for this region).—IRIAN JAYA: *Kostermans 2304*, Vogelkop, Arfak Mts., Angi gita lake, Manokwari subdistr., 1900 m, fl., fr., 9-22 Oct. 1948 (BO, L); *Versteegh BW 10312*, Kebar valley, Watjetoni Mt., 1200 m, 23 Nov. 1960 (L); *Sijde BW 5588*, ibid., Tobi Mts., 1000 m, fl., 18 June 1958 (L); *Brass & Versteegh 11908*, 15 km SW of Bernhard Camp, Idenburg R., 1750 m, fr., 11 Jan. 1939 (A, BM, BO, K, L).—PAPUA NEW GUINEA: ***West Sepik***: *Frodin UPNG 4233*, Aitape subdistr., ridge on Aitape side of Mt. Somero, Torricelli Range, 1200 m, st., 2 Feb. 1974 (K, L). ***East Sepik***: *Hoogland & Craven 10952*, E ridge of Sumset (Mt. Hunstein), Ambunti subdistr., 4500 ft., st., 12 Aug. 1966 (CANB, L); *Takeuchi 6340*, Hunstein Range, Mt. Samsai, 1000+ m, fr., 24 July 1990 (A). ***Madang***: *Pullen 6131*, S slopes Finisterre Range to S of Mt. Abilala, 8100 ft., fr., 17 Nov. 1964 (BM, CANB). ***Southern Highlands***: *Croft et al. LAE 61048*, 2 miles N Iaro R., S slope Mt. Giluwe, Mendi subdistr., 2340 m, fr., 21 Jan. 1974 (A, K, L). ***Enga***: *Flenley ANU 2391*, 4 miles NW of Kupalis, nr. Wabag, 8400 ft., buds, 16 Jan. 1965 (A, K, L); *Hoogland & Schodde 7254*, nr. Kepilan village, Lagaip valley, Laiagam subdistr., 8000 ft., fl., 30 July

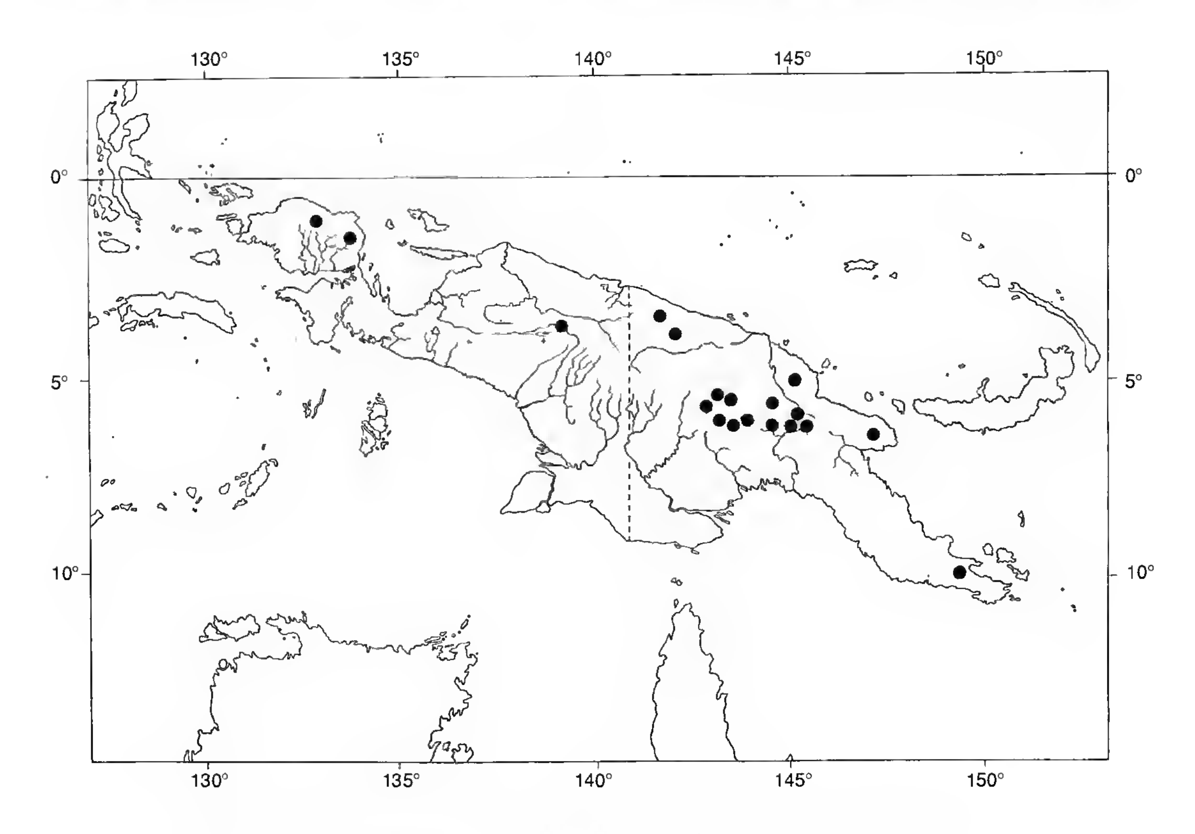


Fig. 3.—Distribution of ***Weinmannia urdanetensis*** in New Guinea (see also HOPKINS 1998b, Fig. 7).

1960 (A, BISH, BM, L); *Saunders 1008*, R.C. Mission Timber lease, Wabag-Komiam rd., Wabag subdistr., 7900 ft., st., juv., 15 July 1960 (CANB, L); *Womersley NGF 15240*, Wabag-Laiagam rd., 24 miles, margin L. Iviva, 1 mile SE Sirunke, 9000 ft., fl., 22 July 1962 (A, K, L). ***Western Highlands***: *Bowers 401*, Hagen subdistr., Pokaripuku, Kopaka, upper Kaugel, 7600 ft., fl., fr., 24 Nov. 1968 (L); *van Royen NGF 18168*, confluence of Warapuri & Kori rivers, Wahgi-Jimmi divide, N of Nondugl, Minj subdistr., 7200 ft., buds, 4 Sep. 1963 (A, BISH, K, L); *Saunders 627*, lower slopes of Mt. Hagen, 2 miles NW of Tomba, 8000 ft., fl., fr., 28 June 1957 (A, L); *Saunders 675*, top Mt. Oga, 8500 ft., st., 12 July 1957 (A, L); *Vinas UPNG 4988*, Mt. Ambrangaba, NE of Milep village, Minj distr., 2350 m, fl., 21 Feb. 1981 (L); *Womersley NGF 5352*, Al R., Nondugl, st., 7 July 1953 (A, BO, K, L, SING). ***Simbu***: *Brass 30306*, Mt. Wilhelm, E slopes, 2770 m, fr., 3 July 1959 (A, K, L); *Sterly 80-40*, Chimbu valley, Gurugaro Ongo, 2500 m, fl., 14 July 1980 (A, L); *Wade ANU 7663*, Keglsugl area, Upper Chimbu valley, 9000 ft., fl., 20 June 1967 (A, CANB, K, L). ***Eastern Highlands***: *Grubb & Edwards 391*, W of Fatima R., Marafunga sawmill, Goroka subdistr., 2600 m, yfr., 25 July 1971 (L); *Hoogland & Pullen 5463*, nr. Daulo camp, Asaro-Mairi divide, Goroka subdistr., 2500 m, fl., 26 June 1956 (A, BISH, BM, CANB, K, L); *Hartley 13274*, Marafunga, 20 miles NW of Goroka, 9500 ft., st., 13 Oct. 1964 (A, CANB, K). ***Morobe***: *Hoogland 9668*, Mannasat, Cromwell Mts., Huon Peninsula, 7900 ft., st., juv., 22 Aug. 1964 (CANB); *Schodde & Craven 4976*, E slope of Spreader Divide, 8 miles NW of Aseki, 7400 ft., st., 18 Apr. 1966 (L). ***Milne Bay***: *Pullen 7857*, Mt. Wadimana ridge, NE from Mt. Simpson, 1770 m, st., 22 July 1969 (L).

LOCAL NAMES.—Asro (Kebar language, Vogelkop); Ain, Jine, Kain (Wahgi language, Minj); Dekiso (Naho language, Finisterre Mts.); Kain-tachai (Enga); Kumare (Chimbu) Kumare yaundo kembre (Kuman language, Chimbu); Kumai (Hagen, Togoba); Dzahamehgehtalalawa (Dunantina); Duasegeh (Chimbu, Masul); Tagantagan (Enga language, Kepilam); Pone-Kuni (Western Highlands?); Q-anak (nr. Wabag, Merimanta); Yambabengo (Chimbu); Uspa (Waskuku, Mt. Hunstein).

GEOGRAPHICAL VARIATION.—Specimens from the western part of the distribution tend to have more numerous pairs of longer, narrower leaflets (Philippines and Irian Jaya; also Torricellis and Mt. Hunstein but the latter are sterile). In the Central Highlands of PNG, leaflets on fertile specimens tend to be shorter and broader, often more densely pubescent ("*W. trichophora*") and there are fewer pairs per leaf. A number of specimens from the Central Highlands have comparatively large leaflets, approaching *W. pullei*; most of these collections are sterile and some show a range in variation in leaflet size on one sheet. Fertile collections with large leaflets include: *Robbins 191*, *Hoogland & Schodde 7254* and *Womersley NGF 11280*.

RELATIONSHIPS.—Apparently closely related to *W. pullei* from New Guinea and *W. clemensiae* from Mt. Kinabalu in Borneo, which it resembles in its branching pattern and somewhat bullate leaflets.

4. Weinmannia croftii H.C. Hopkins, sp. nov.

Weinmannia denhamii Seem. *et* W. vitiensis Seem. *affinis sed ab illa foliolis lateralibus uno usque tribus (non uno usque duodecimis) paribus dispositis, maximis per folio 2.9-6.7 × 0.9-1.7 cm (non 1.1 × 3(-4.8) × 0.3-1.1(-1.5) cm) differt, et ab hac quae folia trifoliolata foliolis latioribus et magnis coriaceis possedet.*

TYPE.—*C.E. Ridsdale NGF 36706*, Papua New Guinea, Madang Prov., Karkar Island, 4°40'S-145°57'E, 3000 ft., fl., yfr., 22 Jan. 1968 (holo-, L!; iso-, A!, BISH!, K!).

Shrub or tree, 2-20 m high. Young twigs shortly hairy, finely ridged with narrow longitudinal fissures and round or elliptical lenticels; branching sometimes dichotomous. Stipules usually caducous on reproductive branches, sometimes persistent on vegetative ones, usually elliptical, ligulate or rhomboidal, ca. 0.7 × 0.4 cm, obtuse to broadly acute at apex, ± glabrous on adaxial surface, strigose on abaxial surface, densely so towards the base. Leaves trifoliolate or imparipinnate with 1-3 pairs of leaflets, up to 14 cm long including petiole of 1.3-2.5 cm; rachis segments 0.8-1.7 cm long; petiole and rachis segments semiterete, flattened above with a narrow central ridge and winged, the wings extending ca. 1 mm on either side, in each rachis segment the wings broader distally towards point of insertion of opposite leaflets; petiole and rachis usually bearded above, glabrous or bearing a few hairs on underside; lateral leaflets lanceolate to narrowly elliptical, the proximal ones often shorter than

the more distal ones when in several pairs, 2.9-6.7 × 0.9-1.7 cm, apex acute, base asymmetrical, the distal side acute to attenuate, proximal side obtuse; terminal leaflet narrowly elliptical to narrowly obovate (2.8-)4.3-11 × (0.9-)1.2-2.3 cm, apex acute, base attenuate; blade glabrous on both surfaces, usually punctate below, subcoriaceous to coriaceous; margin somewhat thickened and minutely revolute, crenate especially towards the apex with 14-17 crenations on each side; midrib narrowly prominent above and slightly prominent below, sometimes hirsute.

Inflorescence a central triad or usually pentad, the lower racemes in the axils of leaves or not; peduncles and rachis segments 0.9-1.6 cm long; racemes 5-9 cm long; inflorescences axes puberulent. Floral buds inserted singly; floral bracts lanceolate or somewhat carinate, up to 2 mm long, somewhat strigose, caducous. Flowers unisexual; pedicel 1-2 mm long, puberulent; calyx lobes triangular, 0.7-1.1 × 0.6-0.9 mm, ± glabrous; petals elliptical, 1.1-1.7 × 0.7-1 mm; disc lobes 0.4-0.8 mm long; in male flowers: filaments 2.4-3 mm long, ovary 0.6-1 mm long ± glabrous, styles minute, 0.2 mm long and curved inwards; in female flowers: filaments 0.9-2 mm long, ovary 1-1.8 mm long, almost glabrous, styles 0.9-1.5 mm long, stigmas capitate and papillose.

Capsules distinctly supported by receptacle, valves 2-4 × 1.3-1.8 mm at dehiscence, the styles 0.8-1.3 mm long; exocarp minutely ridged, almost glabrous (few minute strigose hairs); calyx lobes not persistent; central column present and often persistent on receptacle after valves have fallen. Seeds 0.8-1 mm long, 16 per capsule, comose at both ends, the hairs ca. 0.5 mm long.—Fig. 4A-E, 5.

Breeding system.—Dioecious.

Field characters.—Shrub in open areas such as scoria slopes, or a tree in forest. Flowers white or cream: calyx pale green, corolla and filaments

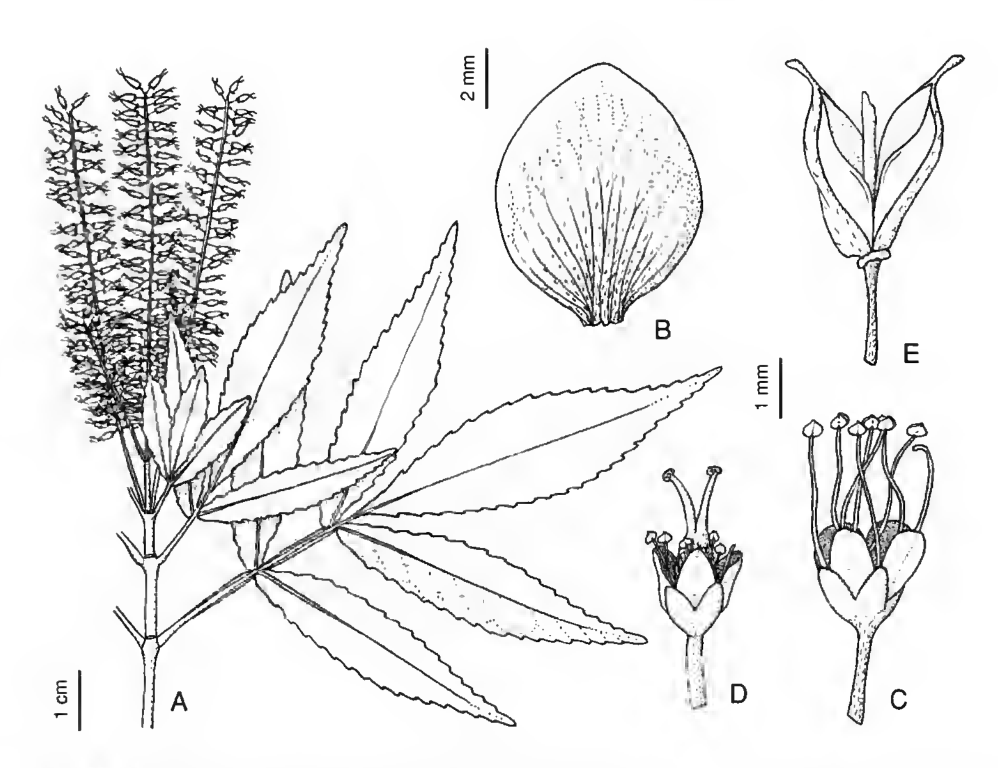


Fig. 4.—***Weinmannia croftii***: **A**, stem showing infructescence (pentad) with reduced leaf at node; **B**, stipule; **C**, male flower; **D**, female flower; **E**, dehisced capsule. (A, *Foreman & Katik LAE 59132*; B, *Frodin NGF 26810*; C, *Ridsdale NGF 36706*; D, *Croft & Katik NGF 14957*; E, *Vandenberg & Mann NGF 42302*).—Drawn by C. Monnié.

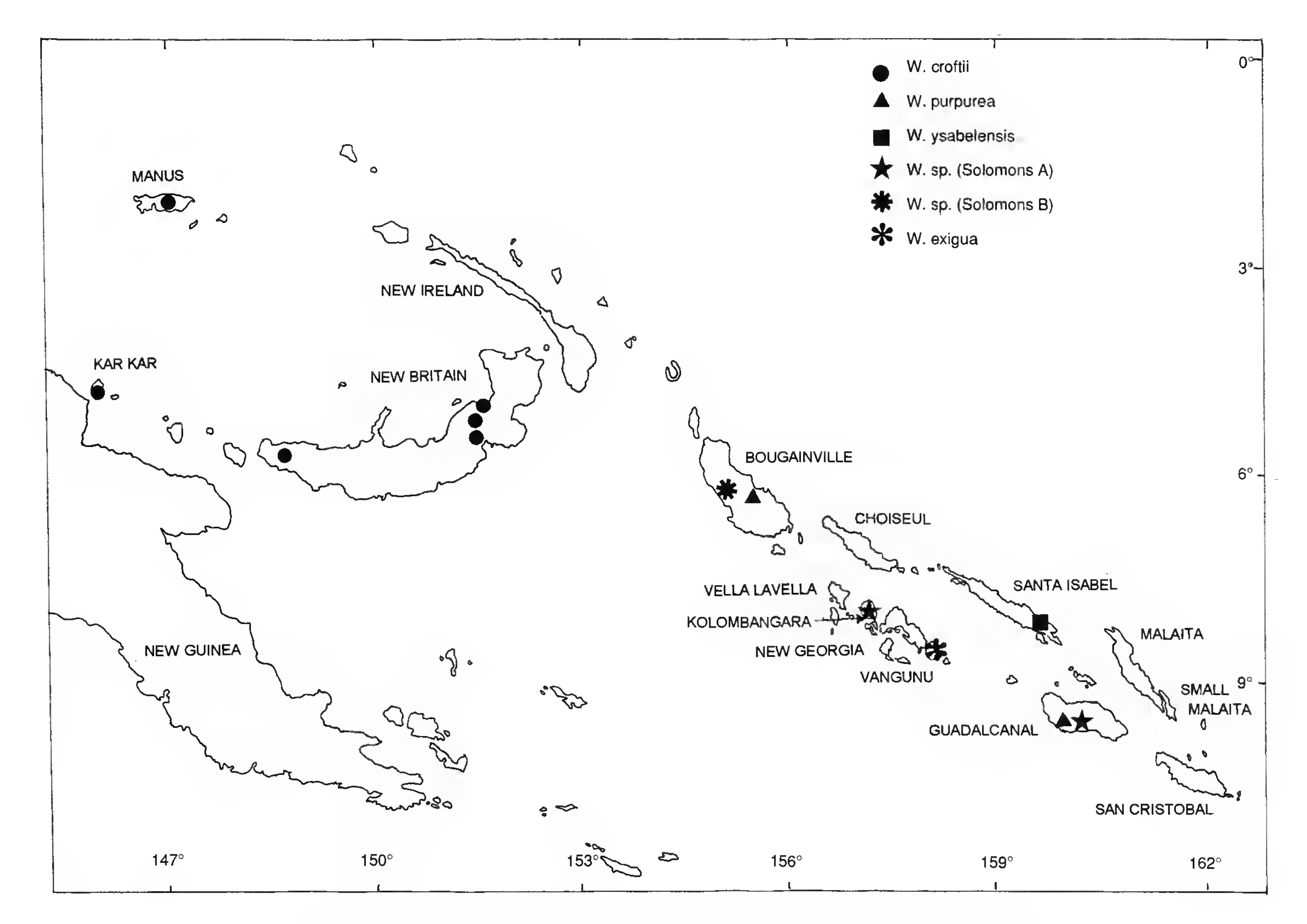


Fig. 5.—Distribution of ***Weinmannia*** in the Bismarck Archipelago and Solomon Islands (except *W. fraxinea*).

white, anthers yellow or straw, disc yellow-orange, ovary light green, stigmas white to brown.

DISTRIBUTION AND ECOLOGY.—Papua New Guinea: Karkar Island, Manus and New Britain. In New Britain, collected from 1200-2100 m, where it is an early coloniser on volcanic substrates as they become stable after an eruption, and sometimes very abundant e.g. on Mt. Ulawon (D. FRODIN pers. comm.). Also found on non-volcanic substrate in mossy montane *Nothofagus* forest where its associates include *Nastus* and *Gleichenia*; soils include clay over limestone. On Manus, collected from 530-720 m and on Karkar, from 820-1050 m in lower montane ridge forest with *Eugenia*, *Pandanus*, *Dillenia*, and *Elaeocarpus*, and a colonist on lava flows where it was co-dominant with *Dodonaea* and *Eurya*. Not yet recorded from New Ireland, where *Weinmannia fraxinea* is found. *Weinmannia croftii* and *W. fraxinea* are sympatric only in New Britain.

PARATYPES.—**PAPUA NEW GUINEA: Bismarck Archipelago**: ***East New Britain***: *Clunie LAE 63017*, nr. lake, central Nakanai plateau, Pomio subdistr., 5°32'S-151°18'E, 1200 m, fl., 28 Nov. 1974 (A, BISH, K, L); *Croft & Katik NGF 14957*, Mt. Sule, ca. 25 miles NNE of Fullerborn Harbour, Pomio subdistr., 5°50'S-150°50'E, 1500 m, fr., 8 May 1973 (A, K, L); *Isles et al. NGF 34406*, Mt. Lululua, ca. 30 miles NE of Fullerborn Harbour, Pomio subdistr., 5°45'S-150°50'E, 2000 m, fl., 11 May 1973 (A, BISH, K, L). ***West New Britain***: *Frodin NGF 26810*, Mt. Talawe, summit, Talasea, 5°32'S-148°18'E, 6400 ft., fl., 25 May 1966 (A, L); *Stevens LAE 51252*, NNE slope Mt. Ulawon, Hoskins subdistr., 5°2'S-151°22'E, 3600 ft., buds, 20 Feb. 1971 (A, K, L); *Vinas LAE 59724*, Lake in Nakanai Plateau, E Nakanai, 5°29'S-151°16'E, 1610 m, fl., fr., 11 Nov. 1975 (A, BISH, BM, K, L). ***Manus***: *Foreman & Katik LAE 59132*, Mt. Dremsel, Lorengau subprovr., 2°15'S-149°50'E, 600 m, fl., 25 Oct. 1974 (A, L); *Kerenga et al. LAE 77543*, ibid., 2°09'S-146°56'30"E, 530 m, fl., 26 Mar. 1981 (A, K, L); *Stone & Streimann LAE 53681*, ibid., 2°10'S-146°55'E, 1800-2000 ft., yfr., 21 June 1971 (A, BISH, L); *Sands et al. 2903*, Mt. Dremsel, 2°08'S-146°57'E, ca. 6 km inland from Pelekawa, fr., 29 Nov. 1975 (K). **NE New Guinea**: ***Madang, Karkar Island***: *Ridsdale NGF 33981*, 4°40'S-145°57'E, 2500 ft., fr., 16 Jan. 1968 (A, BISH, K, L); *Vandenberg & Mann NGF 42302*, 4°40'S-146°00'E, 3200 ft., 12 June 1969 (L).

LOCAL NAMES.—Naligugu (*Frodin NGF 26810*, New Britain), Sirikat (*Ridsdale NGF 36706*, Karkar).

RELATIONSHIPS.—Appears to be closely related to *Weinmannia denhamii* from Vanuatu and *W. vitiensis* from Fiji and possibly conspecific with *Weinmannia sp. A* from the Solomons. All have imparipinnate, coriaceous leaves with a winged petiole and predominantly unisexual flowers. *Weinmannia denhamii* usually has more numerous, shorter leaflets than *W. croftii*, and *W. vitiensis* has trifoliolate leaves with rather broader leaflets than those of *W. croftii*. The three are kept separate for the present since the populations are disjunct and the mean values of the foliage characters are different for each species, even though the ranges overlap.

This species is named after Jim CROFT, formerly at LAE.

Insufficiently known species

Weinmannia sp. (New Guinea A)

Lam 1869 (Irian Jaya, Doormantop, 3100 m, fl., 30 Oct. 1920 [BO, L!]) is from a shrub 0.5 m high; leaves trifoliolate; leaflets orbicular, rounded at apex, coriaceous; margins minutely notched; leaflets, petioles and stems densely hairy.

This collection appears to be a *Weinmannia* but it does not match any described taxon, and fertile material is needed before it can be named. It is most similar to *van Royen & Sleumer 7224* from the Vogelkop (which is placed here in *W. pullei*) but that specimen is almost glabrous and its leaflets are more obovate.

II. WEINMANNIA IN THE SOLOMON ISLANDS (INCLUDING BOUGAINVILLE)

Six species occur in this region: *Weinmannia purpurea*, *W. sp. A* and *W. sp. B* in sect. *Leiospermum*; and *W. fraxinea*, *W. ysabelensis* and *W. exigua* in sect. *Fasciculata*. Except for *W. fraxinea*, most species are known from few collections. Bougainville in particular appears to be

undercollected and *W. fraxinea* has not yet been reported from there. *Weinmannia exigua* also occurs in Fiji (see p. 94 for description) whereas the other four species are endemic.

Key to the species of the Solomon Islands

1. Flowers inserted singly in the axils of bracts on the axes of the racemes; inflorescence usually a triad or pentad; if leaves compound, then rachis winged, the wings extending > 0.7 mm on either side of midline of petiole and rachis 2
1'. Flowers inserted in small fascicles in the axils of bracts on axes of the racemes; inflorescence of 1 or 2 pairs of dyads or tetrads inserted in series at most distal leaf-bearing node; leaves compound and if rachis winged, then wings extending < 0.4 mm on either side of midline of petiole and rachis 4
2. Leaves usually simple (rarely trifoliolate) and relatively large ([3-] 4.2-18 × 1.3-5 cm) .... **4. W. purpurea**
2'. Leaves trifoliolate or imparipinnate, leaflets < 5.5 × 2 cm 3
3. Lateral leaflets 1-2 pairs, 2.5-3.8 × 1-1.5 cm .... **5. W. sp. A**
3'. Lateral leaflets 3-5 pairs, 0.7-1.3 × 0.4-0.5 cm .... **6. W. sp. B**
4. Lateral leaflets (1-)2-4 pairs, 3.5-9 × 1-2.7 cm; rachis terete to semiterete, not winged ...... **1. W. fraxinea**
4'. Lateral leaflets 1-5 pairs, 1.3-2 × 0.7-0.8 cm; rachis minutely winged (wings extending < 0.2 mm on either side of midline) .... **2. W. ysabelensis**
4''. Lateral leaflets 6-9 pairs, 0.9-1.3 × 0.4-0.5 cm, rachis narrowly winged (wings extending < 0.4 mm on either side of midline) .... **3. W. exigua**

1. Weinmannia fraxinea (D. Don) Miq.

For synonomy, description, illustration and distribution map see HOPKINS (1998a, p. 23).

BREEDING SYSTEM.—Flowers bisexual in the Solomons, though the anthers are unusually small (ca. 0.25 mm diameter).

FIELD CHARACTERS.—Tree up to 40 m high, often with plank-like buttresses up to 2 m high. Bark variable: reddish brown and flaking, light brown and fissured, dark brown and scaly, or smooth. Slash also variable: slash wood reported as reddish brown, light brown, pink, white, whitish brown or red, the texture hard, soft, or coarsely fibrous; a detailed description is given on *Walker & White BSIP 150* (A). Buds reddish; flowers white (rarely cream, yellow, light brown), scented or not.

DISTRIBUTION AND ECOLOGY.—Malesia (except Sulawesi and Philippines) to Solomon Islands. See HOPKINS 1998a, Fig. 8, p. 29. Not yet recorded from Bougainville or Makira. From 10-620 m, in well drained primary and secondary forest, often on ridge tops; also in forest over coral limestone, including disturbed forest, flat plain, and forest-grassland boundary.

MATERIAL EXAMINED.—**SOLOMON ISLANDS**: ***Choiseul***: *Gafui BSIP 18977*, SE, W of Oaka River, 1800 ft., fr., 12 Mar. 1970 (L). ***Vella Lavella***: *Kotali BSIP 11173*, S, Oula R. area, 360 ft., fl., fr., 13 Aug. 68 (K, L). ***Kolombangara***: *Mauriasi et al. BSIP 8603*, NE, Kokove Area, 1300 ft., fl., yfr., 12 Jan. 1968 (K, L); *Mauriasi et al. BSIP 8687*, N, Shoulder Hill Area, 400 ft., fr., 19 Jan. 1968 (K, L); *Mauriasi et al. BSIP 11361*, SE, 2000 ft., buds, 6 June 68 (K, L); *Mauriasi et al. BSIP 11493*, SE, Shoulder Hill Area, 800 ft., fl., 17 June 68 (K, L); *Mauriasi et al. BSIP 11647*, NW, Rei Area, 900 ft., fr., 3 July 1968 (K, L); *Whitmore & Womersley BSIP 838*, SE, Bambari Harbour, fl., 24 Nov. 1962 (K, L); *Whitmore BSIP 1436*, W coast, Merusu Cove, 340 ft., fl., 14 Feb. 63 (K, L). ***New Georgia***: *Burn-Murdoch's collectors BSIP 6939*, SE, Mala, fl., 26 Oct. 1966 (K, L); *Cowmeadow BSIP 3690*, NW, Vaimbu R., 230 ft., fl., fr., 18 Mar. 1964 (K, L); *Whitmore's collectors BSIP 3737*, NW, nr. Hovoro, 565 ft., buds, 21 May 1964 (K, L). ***Vangunu***: *Maenu'u BSIP 6420*, Davala, 160 ft., fl., 22 July 1965 (K, L); *Whitmore BSIP 871*, SE coast between Vura village and Gevala R., fl., 29 Nov. 1962 (K, L); *Whitmore BSIP 946*, SE coast between Vura village and Gevala R., inland nr. Merusu Islet, 3 Dec. 1962 (K, L). ***Santa Isabel***: *Beer's collectors BSIP 5124*, NW, Kolokofa R., 20 ft., fr., 1 Apr. 1966 (K, L); *Susui BSIP 8319*, Allardyce Harbour, 30 ft., buds, 17 Nov. 1967 (K, L). ***Guadalcanal***: *Gafui et al. BSIP 9442*, E, ridge S of Makina Station, 120 ft., buds, fr., 14 May 1968 (K, L); *Kere BSIP 4909*, NW, Mt. Mambulu, 1500-1600 ft., fr., 17 Nov. 1964 (K, L); *Lipaqeto BSIP 3376*, NE, Rere R., ca. 3 miles inland, fr., 21 Nov. 1963 (K, L); *Mauriasi et al. BSIP 11823*, E, Makina Area, 180 ft., buds, yfr., 29 Sep. 1968 (K, L); *Mauriasi et al. BSIP 12221*, SW, Wanderer Bay Area, 800 ft., fl., 18 Oct. 1968 (K, L); *Nakisis & Mauriasi BSIP 8122*, NW, E of Mt. Mambulu, 1000

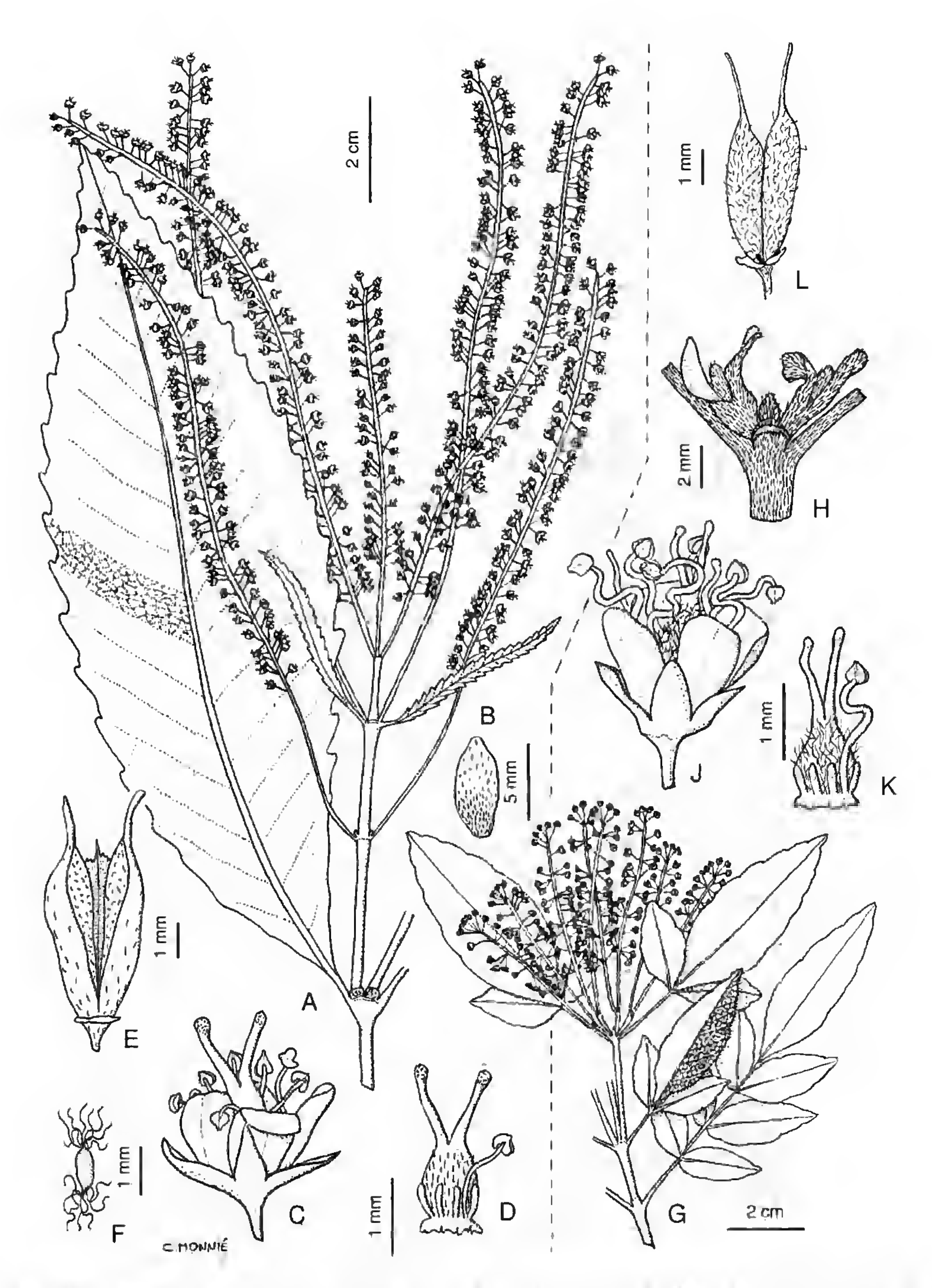


Fig. 6.—**A-F**, ***Weinmannia purpurea***: **A**, left side of a flowering shoot with opposite unifoliolate leaves and one of two partial inflorescences, (heptad) that has reduced leaves at one node; **B**, stipule; **C**, female flower; **D**, detail of C with perianth removed to show gynoecium, disc lobes and one stamen; **E**, capsule at dehiscence with central column; **F**, seed. (A, C, D, F, *Kajewski 1738*; B, E, *Mauriasi BSIP 12092*).—**G-L**, ***Weinmannia ysabelensis***: **G**, flowering shoot with inflorescence of four dyads; note apical bud between inner pair of dyads; **H**, detail of a node showing dormant apical bud and two axillary buds starting to develop, and the bases of two opposite petioles; note stipular scar beneath apical bud; **J**, bisexual flower; **K**, detail of J with perianth removed to show gynoecium, disc lobes and single stamen; **L**, fruit. (A-L, *Brass 3215*).—Drawn by C. MONNIÉ.

ft., fl., yfr., 14 Nov. 1967 (A, K, L); *Sirute'e et al. BSIP 9900*, SE, nr. Logu Village (Avu Avu), 1900 ft., fl., fr., 1 June 1968 (K, L); *Sirute'e et al. BSIP 10074*, W coast, Alidavata (Talise) Kiki Ridge, Duidui, 1000 ft., fl., 13 June 1968 (K, L); *Whitmore BSIP 1283*, Honiara, Mt. Austen, yfr., 31 Dec. 1962 (K, L). ***Malaita***: *Fa'arodo et al. BSIP 13492*, NE, 450 ft., fl., fr., 22 Nov. 1968 (K, L); *Whitmore BSIP 3874*, SW, Are Are district, W coast, Kiu, fl., 13 Dec. 1963 (K, L). ***Small Malaita***: *Gafui et al. BSIP 16322*, Waiusuusu Area, 170 ft., fl., 26 Aug. 1969 (K, L).

LOCAL NAMES.—Aitoto (Kwara'ae) commonly recorded; other names are Futankwai and Wangalu (both Kwara'ae names), Oliolimwani.

DISCUSSION.—Although this is the most commonly collected species from the Solomons Islands, most of the collections date from the 1960s and this species was not recorded from here by BERNARDI (1964). Material from the Solomons is rather uniform.

2. Weinmannia ysabelensis L.M. Perry

J. Arnold Arbor. 30: 162 (1949); Bernardi, Bot. Jahrb. Syst. 83, 183 (1964).—Type: *Brass 3215*, Solomon Islands, Ysabel, Tiratona, 600 m, mountain forest, Nov. 1932 (holo-, A!; iso-, BISH, BM!, BRI, BO!, G, L!, SING!).

Tree 25 m tall. Young twigs densely pubescent, the hairs to 0.4 mm long; older twigs sparsely pubescent; branching not dichotomous. Stipules caducous, ca. 3.5 mm long, sericeous, apex rounded. Leaves imparipinnate, with 1-5 pairs of lateral leaflets, up to 9 cm long, including petiole; petiole and rachis segments 0.5-1.3 cm long, semiterete, sparsely hairy along midline on adaxial side, hirsute on abaxial side, minutely winged, the wings extending 0.2 mm on either side; lateral leaflets ovate to oblong, 1.3-2 × 0.7-0.8 cm, the most proximal ones smaller than more distal ones, apex broadly acute, base somewhat unequal to dimidiatus; apical leaflets narrowly ovate-elliptical, 3-4.4 × 1-1.3 cm, larger than lateral leaflets, apex acute, base often abruptly constricted into decurrent petiolule; blades glabrous on both sides except for hairs ca. 0.5 mm long on midrib on adaxial surface, not punctate; margin somewhat thickened and crenate, 4-6 or 8-9 crenations on each side of lateral and apical leaflets respectively; midrib minutely indented above and prominent below.

Inflorescence of 2 or 4 pairs of dyads; apical bud of the main stem between the bases of the central peduncles sericeous; bud at apex of peduncles between bases of racemes minute, velutinous; peduncles 0.3-0.7 cm long, racemes up to 8 cm long; inflorescence axes puberulent. Flowers inserted in fascicles or singly, especially distally. Flowers bisexual; pedicel 1.5-2.3 mm long, sparsely puberulent; calyx ca. 0.5 × 0.4 mm, glabrous; petals obovate or oblong, 1.3 × 0.8 mm, apex rounded or emarginate; disc lobes up to ca. 0.3 mm long; filaments ca. 3.5 (-4.5) mm long; ovary ca. 0.9 mm long, pubescent; styles up to 1.7 mm long; stigmas papillose.

Immature capsules with ovary 2.8-3.5 × 1.5 mm, exocarp pubescent, the styles 0.8-2 mm long; calyx and disc lobes mostly persistent. Immature seeds ca. 20 per capsule, comose at both ends.—Fig. 5, 6G-L.

BREEDING SYSTEM.—Hermaphroditic.

FIELD CHARACTERS.—Large tree with a thick bole. Bark reddish brown and flaky, the wood hard and red. Flowers white, immature fruits pink.

DISTRIBUTION AND ECOLOGY.—Known only from the type from Ysabel Island where it is described as common.

This species appears closely related to *Weinmannia fraxinea* although the leaflets are much smaller. Further collections are needed to determine the precise relationship between these two species.

PERRY recorded that the seeds had hairs all over their surface (as in *W. pullei* and *W. urdanetensis*) and not only at the ends. The holotype from A has a packet attached with a mature fruit and a seed that matches PERRY's description. However, the fruit is much older than those attached to the twigs with leaves on the sheet, and the seeds the latter contains are immature and have hairs only at the ends. It seems doubtful therefore that the seed described by PERRY was actually from this specimen.

3. Weinmannia exigua A.C. Sm.

For typification, description, illusrration and breeding system see under Fiji (p. 94).

FIELD NOTES.—Common tree up to 20 m high (BRADFORD pers. comm.), with dense rounded crown and flowers in off-white panicles (*Whitmore BSIP 995*).

DISTRIBUTION AND ECOLOGY.—Originally described from Fiji where it is known from two collections. Said to be common on crarer rim on Van(g)unu Island at 2000 ft., on ridge wirh deep humus (*Whitmore BSIP 995*).—Fig. 5, 9A-C.

MATERIAL EXAMINED.—**SOLOMON ISLANDS:** ***New Georgia Group***: *Whitmore BSIP 995*, Van(g)unu Island, inland from Merusu Islet, on narrow parts of ridge with deep humus layer, crater rim, alt. 2000 ft., fl., 10 Dec. 1962 (L!, LAE).

LOCAL NAME.—Wangulu (Kwara'ae) (*Whitmore BSIP 995*).

Whitmore BSIP 995 was previously equared with *Weinmannia urdanetensis* (WHITMORE 1966) which occurs in New Guinea and rhe Philippines, but the leaflet shape is nor a close match. It is similar to the material from Fiji in the size, shape and texture of the leaflets and the narrowly winged rachis, and agrees well with *Howard 89* in the number of pairs of leaflets. The leaflers are also similar in shape to those of *W. ysabelensis* although they are smaller and more numerous (ca. 8 pairs).

4. Weinmannia purpurea L.M. Perry

J. Arnold. Arbor. 30: 159 (1949); Bernardi, Bot. Jahrb. Syst. 83: 198, t. 34 (1964).—Type: *Kajewski 1738* (Papua New Guinea), Bougainville Island, Kupei Gold Field, 1000 m, rain forest, Apr. 1930 (holo-, A; iso-, BISH, BM!, BRI, G, GH, L!, LE, S, SING!, US).

Tree 20 m high. Twigs terete, scarcely flatrened at nodes, branching frequently dichotomous. Internodes up to 8 cm long. Stipules caducous, elliptical, ca. 0.8 × 0.4 mm, apex rounded or obtuse, sparsely strigose on abaxial surface, glabrous on adaxial one. Leaves usually simple or unifoliolate, the petiole articulated at junction with blade or not, or rarely trifoliolate; simple leaves broadly lanceolate or narrowly ovate (3-) 4.2-18 × 1.3-5 cm, apex acute to caudate, base attenuate to decurrent; in unifoliolate and trifoliolate leaves, articulated petiole ca. 1.5 cm long, narrowly winged, sparsely puberulent; in trifoliolate leaves, lateral leaflets ca. 3.5 × 1.2 cm, unequal at base; leaf blade glabrous on both surfaces, punctate below, subcoriaceous; margin somewhat thickened and minutely revolute, strongly crenate (13-)18-25 crenations on each side of the blade; midrib narrowly ridged above and strongly prominent below, secondary and tertiary venation slightly raise on both surfaces.

Inflorescence usually a central penrad (sometimes a triad or heptad) or composed of 2 lateral partial inflorescences, the apical bud aborted; triads somerimes developing in subdistal nodes also; peduncle and rachis segments 1.4-4.5 cm long, racemes up to 17 cm long; inflorescence axes puberulent to almost glabrous. Floral buds inserted singly; floral bracts ± linear, 1.8 mm long, caducous. Flowers unisexual, only female flowers seen, the stamens shortly exserted from the flower and shorter than the styles; pedicel 1-2.1 mm long, puberulent; calyx lobes triangular, 0.8 × 0.5 mm, glabrous; petals ovate, 1.4 × 0.8 mm; disc lobes up to 0.7 mm long; filaments ca. 1.5 mm long, anther 0.3 × 0.3 mm, empty; ovary ca. 1.5 long, sparsely and minutely strigose or ± glabrous; styles 0.9-1.3 mm long; srigmas capitate and papillose.

Capsules 3.1-3.5 × 1.2-1.5 mm at dehiscence, the styles 1.1-1.3 mm; exocarp with minute longitudinal ridges, almost glabrous with a few minute strigose hairs, warty; calyx lobes not persistent; central column present. Seeds ca. 0.8 mm long, 16 per capsule, comose at both ends, the hairs ca. 1 mm long.—Fig. 5, 6A-F.

BREEDING SYSTEM.—Dioecious?

FIELD CHARACTERS.—Bole crooked, ca. 50 cm dbh, buttresses absent. Bark light brown smooth; slash: wood hard, reddish hrown, bark soft. Flowers very pale purple on purple stems (*Kajewski 1738*) or white with a faint smell (*BSIP 12092*). Fruit purple (*Kajewski 1738*),

green when immature (*BSIP 12092*).

DISTRIBUTION AND ECOLOGY.—Known from only two collections, growing at 785-1000 m. Habitats described as rain forest and well drained primary forest on ridge top. Common according to KAJEWSKI.

MATERIAL EXAMINED.—**PAPUA NEW GUINEA:** ***Bougainville***: *Kajewski 1738* (BO, L, P, SING, type).—**SOLOMON ISLANDS:** ***SW Guadalcanal***: *Mauriasi BSIP 12092*, Duidui area, 2400 ft., fl., yfr., 9 Oct. 1968 (K, L).

LOCAL NAME.—Aitoto (Kwara'ae).

Uncertain and little known species

5. Weinmannia sp. (Solomons A)

Weinmannia sp., Corner, Philos. Trans. Ser. B 255: 577 (1969).

Tree up to ca. 8 m high. Stems glabrous, branching sometimes dichotomous. Stipules caducous, ligulate, ca. 4 × 2 mm, with short strigose hairs on the abaxial surface. Leaves trifoliolate or imparipinnate with 2 pairs of lateral leaflets, up to 7.5 cm long, including the petiole; petiole and rachis segments 1-2 cm long, glabrous, winged, the wings extending up to 1 mm on either side of midline; lateral leaflets elliptical, 2.5-3.8 × 1-1.5 cm, base ± unequal, apex acute; terminal leaflets elliptical, 4.5-5.5 × 1.7-2 cm, base attenuate, apex acute; blades glabrous on both surfaces, punctate below, coriaceous; margin crenate (but much chewed by insects).

Inflorescence composed of triads or pentads, sometimes a few successive nodes bearing partial inflorescences simultaneously, and reduced leaves at nodes within the inflorescence. Floral buds inserted singly; floral bracts ca. 2.7 mm long, exceeding buds, ligulate, minutely strigose. Pedicel puberulent; calyx lobes glabrous. Mature flowers and fruits unknown.—Fig. 5.

IMMATURE FOLIAGE.—In *Corner RSS 1188*, the leaves have up to 3 pairs of narrowly elliptical leaflets; young stems, leaf axes and underside of the midrib are puberulent. *Hill RSS 9011* has broadly ovate lateral leaflets and the axes and leaves are glabrous.

FIELD CHARACTERS.—Bark and wood red. Inflorescence in bud red; flowers pinkish (*Corner RSS 89*) or white and sweetly fragrant (J.C. BRADFORD pers. comm.).

DISTRIBUTION AND ECOLOGY.—Collected at 700-900 m on Vangunu (J.C. BRADFORD pers. comm.), 1100-1800 m on Kolombangara (BRADFORD pers. comm. and *Corner RSS 89*) and 2340 m on Guadalcanal (*Hill RSS 9011*). Habitats include forest on summit plateau and ridge of mountains. Common.

MATERIAL EXAMINED.—**SOLOMON ISLANDS:** ***Kolombangara***: *Corner RSS 1188*, 5500 ft., st., 2 Sep. 1965 (K); ***Guadalcanal***: *Corner RSS 89*, Popomanasiu, 7000 ft., fl., 23 Oct. 1965 (K, L); *Hill RSS 9011*, Mt. Popomanasiu, 7000 ft., st., 5 Nov. 1965 (K, L).

LOCAL NAME.—Huta-ana-kwai (*Corner RSS 89*).

The description is based on *Corner RSS 89*, the only fertile collection, because sterile material of *Weinmannia* is notoriously variable and often lacks the distinguishing characters seen in adult plants.

This species belongs to the same group as *Weinmannia croftii* from the Bismarck Archipelago and Karkar Island, *W. denhamii* from Vanuatu, and *W. vitiensis* from Fiji, since all four taxa have a winged petiole and rachis, and an inflorescence consisting of triads or pentads, as frequently see in sect. *Leiospermum*. It may in fact turn out to be conspecific with *W. croftii*, but more fertile collections are needed to determine whether the range in leaflet size and shape for this population is unique.

6. Weinmannia sp. (Solomons B)

Parker 6, from Mt. Bolbi, Bougainville Island, Papua New Guinea, in low forest 10-30 ft. high, 8000 ft., Oct. 1963 (CANB) is a specimen in bud only of an undescribed species belonging to sect. *Leiospermum*.

Young stems hirsute, branching sometimes dichotomous. Stipules not seen. Leaves imparipinnate, with 3-5 pairs of leaflets, up to ca. 5 cm long: petiole and rachis segments 0.4-0.7 cm, hirsute especially on upper surface, winged, the wings extending up to 0.7 mm on either side of the midline; lateral leaflets ± elliptical, 0.7-1.3 × 0.4-0.5 cm, base acute, apex broadly acute; terminal leaflets elliptical, 1.5-1.9 × 0.5-0.6 cm, base attenuate, apex acute; blades coriaceous, glabrous. Floral buds inserted singly on inflorescence axis.—Fig. 5.

III. WEINMANNIA IN VANUATU (with R.D. HOOGLAND[†])

Two species occur in this region, both of them endemic: *Weinmannia denhamii* is widespread and more common than *W. macgillivrayi*. The first belongs to the group of species in sect. *Leiospermum* that have a narrowly winged leaf rachis and are often found on young volcanic soils, where as *W. macgillivrayi* is closely allied to *W. fraxinea* in sect. *Fasciculata*. Both species in Vanuatu have predominantly unisexual flowers and almost glabrous fruits.

Key to the species of Vanuatu

1. Leaf rachis and petiole terete, densely hairy on the upper surface, not winged; lateral leaflets often with small "ears" at point of attachment to leaf rachis; inflorescence of one or more pairs of lateral dyads, the apical bud of main stem persisting and dormant during flowering .... **1. W. macgillivrayi**

1'. Leaf rachis and petiole semiterete, glabrous, winged; lateral leaflets without "ears" at point of attachment to leaf rachis; inflorescence a central triad or pentad sometimes also with lateral triads or additional racemes .... **2. W. denhamii**

1. Weinmannia macgillivrayi Seem.

Fl. Vit.: 109 (1866); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Bernardi, Bot. Jahrb. Syst. 83: 173, t. 22 (1964).—Type: *Milne 277* (Vanuatu), Aneiteum (= Anatom), H.M.S. Herald 1854 (lecto-, here designated, K!).

Small shrub to largish tree, 15-20 m tall. Branching not usually dichotomous. Nodes somewhat laterally flattened, the stipular scar arched on both sides, especially at distal nodes. Stems glabrescent, rarely not, with numerous lenticels and fine longitudinal grooves. Stipules usually caducous, ± orbicular or shortly spathulate, rounded at apex rounded and narrowing towards base, up to 1 × 1.1 cm, sometimes revolute, shortly strigose on abaxial surface, especially towards the base and glabrous on adaxial surface except at base. Leaves imparipinnate with 4-10 (-12) pairs of leaflets, up to 14 cm long including petiole of 10-35 mm; rachis segments 5-9 mm long; petiole and rachis terete or channelled, densely hairy on adaxial surface and in groove, the hairs up to 0.5 mm long, glabrous or with few scattered hairs below (rarely densely hairy all round, *Veillon 3992*); lateral leaflets sessile, narrowly ovate to lanceolate, the lower 1-3 pairs distinctly shorter than the upper pairs but of similar width, up to 2.2-4.6 × 0.6-1.3 cm, apex narrowly acuminate, base unequal, obtuse to rounded, not lying flat on pressing, often 1 or 2 small free auricles ca. 0.6 × 0.4 mm on rachis between bases of opposite leaflets; apical leaflets 2.7-5.5 × 0.9-1.4 cm, narrowly elliptical, the base attenuate, the apex narrowly acuminate to caudate; blades glabrous on both surfaces except for weak hairs ca. 1 mm long on midrib on abaxial surface, not punctate below, subcoriaceous; margin sometimes somewhat thickened or minutely revolute, crenate to serrate especially towards the apex with up to 10 teeth on each side of the largest leaflets; midrib indented above and prominent below, secondary veins ± flat on both surfaces.

Inflorescence of 1 or 2 pairs of dyads, sometimes a few successive nodes producing partial inflorescences simultaneously; peduncles 0.2-0.6 cm long, shortly and sparsely pubescent; apical bud of main stem between central peduncles usually present, sericeous; buds at apex of

peduncles in angle between racemes sericeous, minute; racemes ca. 7-14 cm long, rachis sparsely puberulent. Floral buds inserted in fascicles; floral bracts ligulate or somewhat boat-shaped, 0.4-0.9 mm long, caducous with short, stiff hairs. Flowers unisexual or rarely bisexual; pedicel 1.6-2.8 mm long glabrous or minutely pubescent at base; calyx lobes triangular, 0.6-0.7 × 0.4 mm long, glabrous; petals elliptical-ovate or obovate, 1-1.6 × 0.7-0.8 mm; disc lobes 0.2-0.4 mm long; in male flowers: filaments 2.8-4.2 mm long, ovary small 0.3-0.9 mm, pubescent, the styles 0.4-1.2 mm long and not exserted beyond the anthers; in female flowers: stamens short and not exserted beyond the styles, the filaments up to ca. 1.1 mm long, ovary ca. 1 mm long, pubescent, styles ca. 1.3 mm long, ovules 8 per locule.

Capsules 2-3.5 × 2-2.2 mm at dehiscence, the styles 1.7-2 mm long, the exocarp smooth, almost glabrous with a few weak hairs; calyx lobes persistent; central column weakly developed or absent. Seeds ca. 0.8 mm long, persistent in capsule, usually comose at both ends, the hairs coarse and straw-like, ca. 2 mm long, twisted around seed in capsule.—Fig. 7A-E, 8.

BREEDING SYSTEM.—Polygamodioecious. Most specimens have only either male or female flowers but *Kajewski 735* has male and a few bisexual ones (though the ovary may not be functional as the ovules are minute). In *Schmid 3557* the flowers appear bisexual with a few males ones mixed in.

FIELD CHARACTERS.—Flowers white or cream, fruits reddish.

DISTRIBUTION AND ECOLOGY.—Several collections from Anatom (also known as Aneityum), the southern most of the main islands in the chain, and one from Santo, the largest island, towards the north. Recorded from 30-300 m from scrub, rain forest, open secondary forest and forest on ridge. Described as common (*Kajewski 735*).

MATERIAL EXAMINED.—**VANUATU**: ***Anatom (Aneityum)***: *Bernardi 12974*, nr. Anawounamalo, R. Inwa Lelgey (sic) (= Inwan Leleghei), 10-180 m, st., 5 May 1968 (K, P); *Bourdy 322*, autour d'Anelgahoat (sic), 30 m, fr., 1 Feb. 1986 (K, P); *Cabalion 1944*, W Inwooutié R., 300 m, fl., 18 Mar. 1983 (NOU, P); *Cabalion 1944b*, Anelgaohat, Inwooutié R., Res. Service Forestier, 80 m, fr., 18 Mar. 1983 (NOU, P); *Kajewski 735*, Anelgauhat Bay (sic), 100 fr., buds, 11 Feb. 1929 (A, BISH, K, P); *Roata 14*, fr., 1976 (NOU); *Schmid 3557*, fl., 1 Dec. 1970 (P); *Schmid 5083*, secteur de Anelghanal, fl., fr., Nov. 1974 (NOU); *s.coll.*, *s.n.*, s.loc. (BM, type folder, no label). ***Espiritu Santo***: *Veillon 3992*, direction Voutmele, buds, Aug. 1979 (P).

LOCAL NAMES.—Nomropon (*Bourdy 322*) but see under *Weinmannia denhamii* in WHEATLEY (1992).

TYPIFICATION.—The material of both this species and of *Weinmannia denhamii* described by SEEMANN was collected during the voyage of the H.M.S. HERALD, under the command of Captain H.M. DENHAM. MACGILLIVRAY was the ship's naturalist and MILNE the assistant naturalist before they were dismissed and discharged respectively during the voyage, for dereliction of duty (DAVID 1995). According to DAVID, the Herald visited Aneiteum, where the collections of *Weinmannia* were made, between 7 November 1853 and 1 January 1854, and plant specimens were sent to W. HOOKER at Kew. However, MACGILLIVRAY may have passed some of MILNE's collections off as his own, and HOOKER criticised the poor labelling of the material he received (DAVID 1995). In the description of *W. macgillivrayi*, SEEMANN cited material collected by both MACGILLIVRAY and MILNE, which constitute syntypes; *Milne 277* (K) is designated here as the lectotype. A specimen in a type folder at BM has no label and may or may not belong to the same collection.

RELATIONSHIPS.—This species is a satellite of the widespread Malesian *W. fraxinea*, distinguished from it by more numerous and smaller leaflets and by the ears that are frequent on the leaf rachis at the point of insertion of the lateral leaflets. In both species, the upper surface of the leaf rachis is often densely hairy.

2. Weinmannia denhamii Seem.

Fl. Vit.: 109 (1866), as "denhami"; Engler, Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Bernardi, Bot.

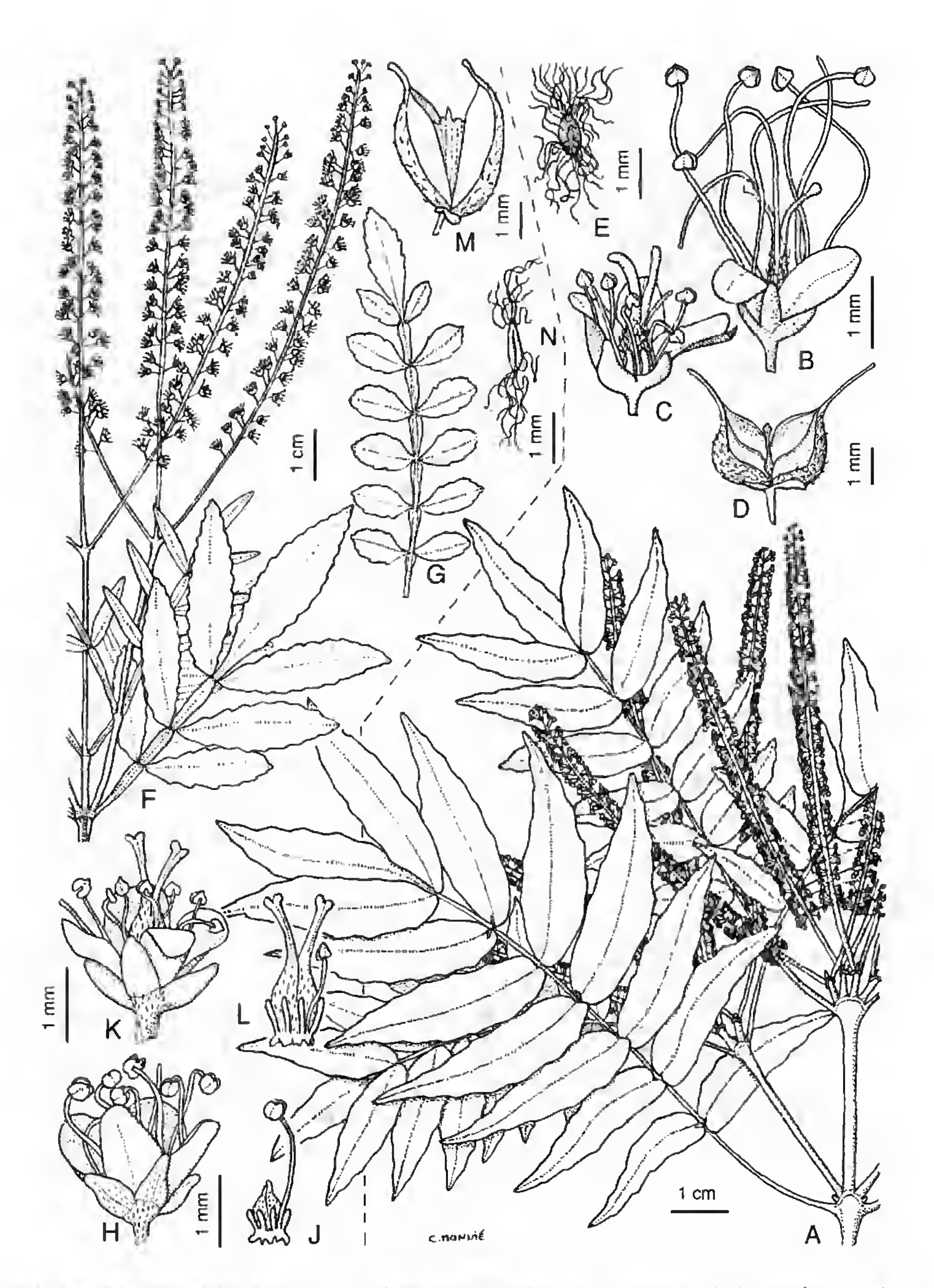


Fig. 7.—**A-E**, ***Weinmannia macgillivrayi***: **A**, part of a flowering shoot with imparipinnate leaves (only one shown) at the most distal node subtending an inflorescence of 4 dyads; more proximal node has a lateral shoot with an inflorescence of two dyads; note minute buds in angle between racemes of each dyad; **B**, flower, probably bisexual; **C**, female flower, one petal removed; **D**, dehisced capsule with persistent calyx lobes; **E**, seed. (A, *Kajewski 735*; B, *Schmid 3557*; C, *Cabalion 1944*; D, E, *Roata 14*).—**F-N**, ***Weinmannia denhamii***: **F**, part of a flowering shoot with central and lateral triads (only one lateral triad shown); note reduced leaves at some nodes within inflorescence; **G**, single leaf with smaller, more numerous, leaflets (type of *W. tannaensis*); **H**, male flower; **J**, detail of H with perianth removed to show gynoecium with very reduced styles, disc lobes and a single stamen; **K**, female flower; **L**, detail of K with perianth removed to show gynoecium with long styles, disc lobes and a single stamen; **M**, capsule at dehiscence, note central column and enlarged receptacle; **N**, seed. (F, *MacGillivray 45*; G, *Kajewski 151*; H, J, M, N, *Aubert De La Rüe* s.n., 2ème Voyage, Jan. 1936; K, *Schmid 5084*).—Drawn by C. MONNIÉ.

Jahrb. Syst. 83: 190, t. 32 (1964); Wheatley, Guide Common Trees Vanuatu: 76, t. 77 (1992).—Type: (*MacGillivray*) *45*, (Vanuatu), Aneiteum (= Anatom), in woods (lecto-, here designated, K!; isolecto-, BM!, G, P! 3 sheets).

Weinmannia kajewskii Guillaumin, J. Arnold Arbor. 12: 250 (1931).—Type: *Kajewski 317* (Vanuatu), Eromanga Island, Dillon Bay, 400 m, rain forest, common, 28 May 1928 (holo-, P!; iso-, A!, BISH!).

Weinmannia tannaensis Guillaumin, J. Arnold Arbor. 12: 251 (1931); Bernardi, Bot. Jahrb. Syst. 83: 178, t. 27 (1964).—Type: *Kajewski 151* (Vanuatu), Tanna Island, Mt. Tokosh Meru, 1000 m, rain forest, common, 15 Mar. 1928 (holo-, P!; iso-, BISH!).

Weinmannia kajewskii Guillaumin var. *ambrymensis* Guillaumin, Bull. Soc. Bot. France 82: 349 (1935), nom. illeg., no Latin description. Collection cited: *Aubert de la Rüe s.n.* (Vanuatu), Ile Ambrym, sur le grande plateau de scories à proximité du volcan actif, cote 600-700, Août 1934 (A!, L!, P!).

Shrub or tree, 2-20 m high, also sometimes an epiphyte or strangler; branching sometimes dichotomous; young twigs shortly hairy, finely ridged with narrow longitudinal fissures and round or elliptical lenticels; older twigs with stipular scars ± horizontal. Stipules usually caducous on reproductive branches, sometimes persistent on vegetative ones, variable in shape, usually ovate or ligulate, 6-10 × 2-4.5 mm, sometimes orbicular (juvenile foliage?), 8-12 × 10-14 mm, rounded or obtuse at apex, glabrous or minutely hairy on adaxial surface, with a few scattered hairs to 0.3 mm long on abaxial surface. Leaves imparipinnate with 1-12 pairs of leaflets, up to 14 cm long including petiole of 7-25 mm; rachis segments 6-13 mm long; petiole and rachis segments semiterete, flattened above with a narrow central ridge and winged, the wings extending 0.5-1.5 mm on either side of mid-line, on each segment the wings broader distally towards point of attachment of leaflets; petiole and rachis glabrous to puberulent above, glabrous or bearing a few hairs on underside especially at point of attachment of leaflets; lateral leaflets lanceolate, elliptical or ovate, the proximal ones often shorter than the more distal ones, 1.1-3(-4.8) × 0.3-1.1(-1.5) cm, apex acute, base asymmetrical, distal side acute to attenuate, proximal side obtuse to rounded; terminal leaflet narrowly elliptical to narrowly obovate 2.1-4.1 (-6.4) × 0.3-1(-1.7) cm, apex acute, base attenuate; in leaves with few pairs of pinnae, terminal leaflet often larger than lateral ones; in leaves with numerous pairs of pinnae, terminal leaflet ± equal length and narrower than lateral ones; blade glabrous on both surfaces, usually punctate below, subcoriaceous; margin somewhat thickened and minutely revolute, crenate especially towards the apex with 6-17 crenations on each side; midrib narrowly prominent above and slightly prominent below, when sometimes minutely hairy.

Inflorescence a central triad or usually pentad, the lower racemes either in the axils of leaves or not, rarely replaced by lateral triads; sometimes a few successive nodes on a shoot bearing partial inflorescences simultaneously; peduncles and rachis segments 0.8-3 cm long; racemes 5-11.5 cm long; inflorescences axes puberulent. Floral buds inserted singly; floral bracts lanceolate or somewhat carinate, up to 1.1 mm long, bearing a few hairs towards base on abaxial surface, caducous. Flowers unisexual; pedicel (1-)1.4-3 mm long, slender, puberulent; calyx lobes triangular, 0.9 × 0.6-0.7 mm, ± glabrous; petals ovate-elliptical, 1.3-1.6 × 0.7-0.9 mm; disc lobes 0.5-0.7 mm long; in male flowers: stamens long and anthers far exserted beyond stigmas, filaments (1.6-)2-3.5 mm long, ovary 0.9-1.1 mm long, styles minute, < 0.1 mm long and curved inwards; in female flowers: stamens short and stigmas exserted beyond anthers, filaments 1-1.7 mm long, ovary 1.3-1.5 mm long, almost glabrous, styles ca. 1 mm long.

Capsules distinctly supported by receptacle, valves 3-4 × 1.7-2 mm at dehiscence, the styles 0.8-1.3 mm long; exocarp with minute longitudinal ridges, almost glabrous with a few minute strigose hairs; calyx lobes not persistent; central column often persistent on receptacle after valves have fallen. Seeds ca. 0.6 mm long, 16 per capsule, tending to persist in capsule after dehiscence, comose at both ends, the hairs 0.8-1 mm long.—Fig. 7F-N, 8.

Breeding system.—Dioecious or polygamodioecious? Most specimens have unisexual flowers but two collections at P (*Aubert de la Rüe s.n.*, 19 Feb. 1936 and *Bernardi 12986*) have both

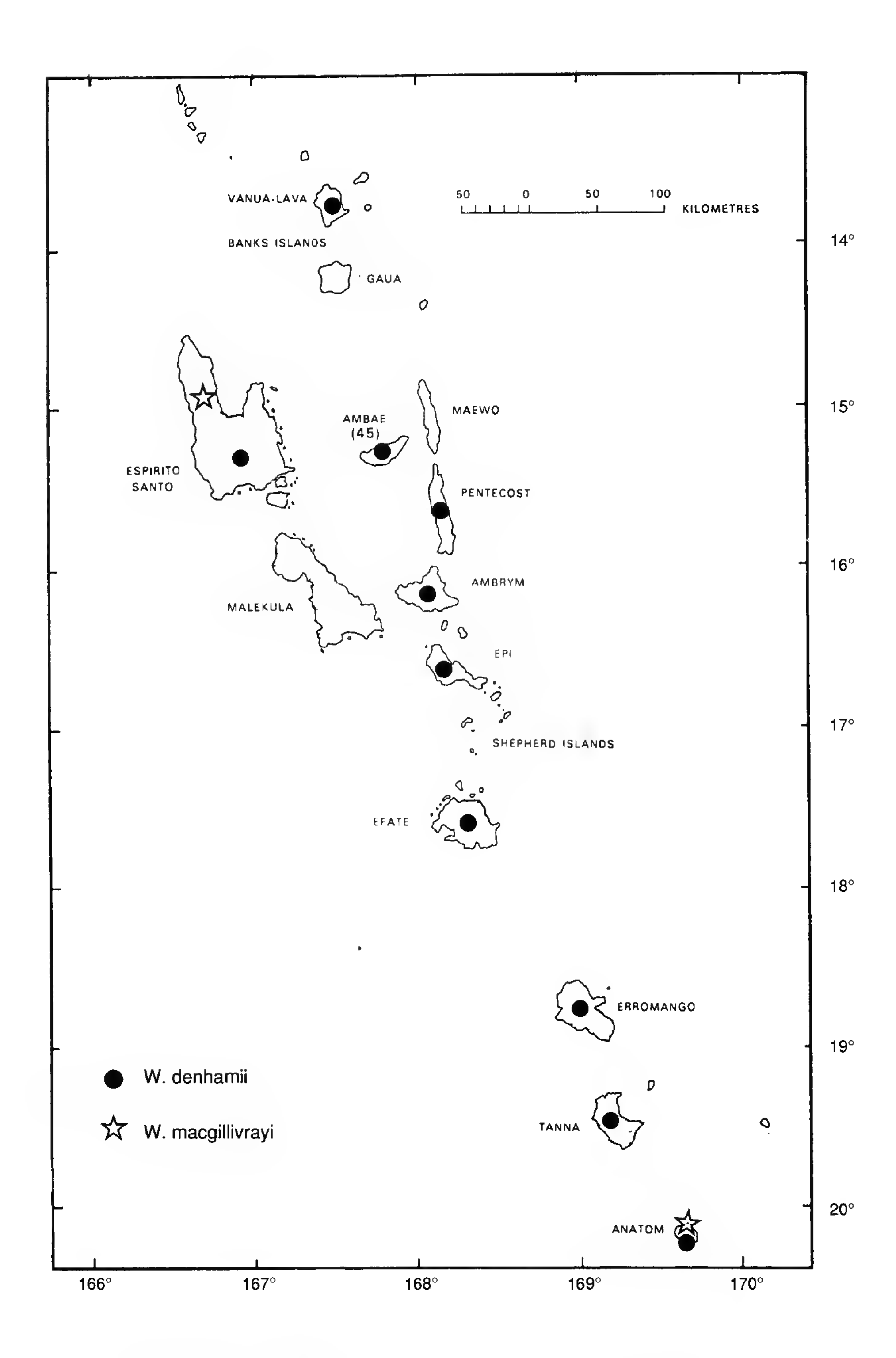


Fig. 8.—Distribution of ***Weinmannia*** in Vanuatu. One symbol per species per island.

male flowers and fruits on the same twig.

GROWTH FORM AND FIELD CHARACTERS.—As in other species whose distribution covers a wide range of elevation, size and growth habit are influenced by altitude and exposure. It is recorded as a tree 20 m high at 1300 m (on Ambae) and as a shrub 2 m high at 1800 m (on Santo). When a large tree, the crown may be open and spreading, flat-topped with the branches vertically ascending to form an inverted cone, or dome-shaped with divaricate branches, the foliage feathery (*Wheatley 207*), in distinct clumps on otherwise bare branches (*Wheatley 55*). The bole is sometimes twisted and leaning. Also described by *Wheatley 207* (and 1992) as a strangler that kills its host and then forms a bole by the fusion of the roots, with a diameter of nearly 70 cm.

Bark light grey or brown-grey, smooth with fine vertical fissures, blackish or reddish on old trunks. Inner bark red or orange, fibrous. Sap wood white, cream to yellowish. Heartwood pink-cream, sweet-smelling. Young leaves flush reddish or yellowish-red, mature leaves dark green and slightly shiny above, silver-green below (*Wheatley 207*). Flowers usually described as white, rarely yellowish-green or pink, and much visited by insects (*Bernardi 12986*). Fruit pink, red then brown.

DISTRIBUTION AND ECOLOGY.—Known from most of the larger islands of Vanuatu. Lowest recorded altitude varies by island but the overall elevation range is 120-1800 m.

According to WHEATLEY (1992), *W. denhamii* is a canopy species of upper middle and high elevation forest where it is co-dominant with *Metrosideros* over large areas. Other habitats include riverine forest on basalt, open woodland with tree ferns, bracken-covered ridge grazed by bullocks, open *Acacia spirorbis* scrub, open secondary forest, and deforested areas with *Pteridium* and *Gleichenia*. At higher elevations it occurs in montane, dwarf forest on exposed crests and ridges.

Soil types recorded from specimens include volcanic cinders and lava, and young brown andosol. Although *W. denhamii* belongs to the group of species (including *W. croftii*, *W. vitiensis* and *W. sp.* Solomons A) that are often found on relatively young volcanic soils, WHEATLEY says it is less frequent than *Metrosideros* on the juvenile ash soils of Tanna and the Ambrym caldera.

MATERIAL EXAMINED.—VANUATU: ***Vanua Lava***: *Wheatley 375*, s.loc., 550 m, fl. (K). (***Espiritu***) ***Santo***: *Cabalion 462*, Col sur le Custom rd., entre R. Pialapa et village Wunabaï, 850 m, fl., 21 Mar. 1978 (NOU); *Chew Wee-Lek RSNH 204*, Mt. Tabwemasana, 1520 m, st., 3-8 Sep. 1971 (K); *Cribb & Wheatley 82*, Saktouy to Tabwemasana, 1500-1550 m, fr., 24 Oct. 1988 (K); *Curry 1640B*, Fortsenale, nr. village, 700 m, fr., 10 Dec. 1994 (K); *Gillison & Beveridge RSNH 3531*, Nokowoula village area, 3500 ft., fr., 28 Aug. 1971 (P); *Raynal RSNH 16345*, Mt. Tabwemasana, 1800 m, fr., 2 Sep. 1971 (K, L); *Veillon 4026*, direction du Voutmele, 1000 m, fr., Aug. 1979 (P). ***Ambae*** (= ***Aoba***): *Quantin in Schmid 1941*, sommet du volcan, 1000 m, st., 18 Nov. 1966 (P); *Wheatley 55*, s.loc., 1300 m, st., 23 Nov. 1988 (K). ***Pentecost***: *Aubert de le Rüe s.n.*, Kumre, 600 m, st., 19 Dec. 1935 (P); *Wheatley 207*, Tambok, 460 m, buds, 9 Feb. 1989 (K). ***Ambrym***: *Aubert de le Rüe s.n.*, Mt. Tollo, 1000 m, st., 5 Jan. 1936 (P); *Aubert de le Rüe s.n.*, 650-800 m, fl., fr., 8-11 Jan. 1936 (L, P); *Aubert de le Rüe s.n.*, Grand plateau autour du Mt. Marum, 700 m, fl., fr., 10 Jan. 1936 (P); *Bourdy 118*, au-dessus de Lalinda, 600 m, fr., 23 Sep. 1985 (K, P). ***Epi***: *Curry 1026*, Mt. Tainaruru, close to summit, S side above Filakara, 500 m, fr., 20 July 1993 (K). ***Efate***: *Schmid 248*, Vate, 450 m, fr., 26 Feb. 1965 (P); *Kajewski 236*, Undine Bay, 500 m, fr., 25 Apr. 1928 (K, P). ***Erromango***: *Aubert de le Rüe s.n.*, W du massif occupant le N de l'île, 400 m, fl., fr., 19 Feb. 1936 (P); *Bernardi 13258*, W, Dillon Bay, Oponhkor, Mt. Menel, R. Nevel, 250-350 m, fr., 3 June 1968 (K, L, P); *Cabalion 1388*, S, Fedmoghum, 300 m, fr., 21 Feb. 1982 (NOU); *Cheesman 34*, s.loc., 1600 ft., fr., 17 July 1930 (K); *Curry 550*, Logging trail from Dillons Bay to Port Narvin, 120 m, fr., 5 Aug. 1992 (K); *Johnson 12*, s.loc., 300 m, fl., s.dat. (K); *Schmid 4740*, Centre, 300 m, buds, fr., 25 June 1973 (NOU); *Schmid 5084*, N de Happy Land, 250 m, fl., 21 Nov. 1974 (NOU). ***Tanna***: *Aubert de le Rüe s.n.*, s.loc., st., Mar. 1934 (P); *Bernardi 12849*, nr. Lootopounga, 250-300 m, buds, 29-30 Apr. 1968 (K, L, P); *Bernardi 12909*, Lamwinaoura, fl., fr., 1-2 May 1968 (K, L, P); *Bernardi 13097*, Pagi Yanehoop, 300 m, fl., fr., 20 May 1968 (K, L, P); *Chew Wee-Lek RSNH 109*, Yerou, SW foot of Mt. Toukousmerou, 100-200 m, fl., fr., 27 July 1971 (K, P); *Morat 5897*, Flan E du Toukosmereu, 500 m, fl., 7 Feb. 1978 (NOU, P); *Morat 6043*, Mt. Toukosmereu, 500-600 m, fr., June 1978 (NOU, P); *Schmid 3176*, vers Côte Est, 500 m, fr., 7 May 1970 (K, NOU, P). ***Anatom*** (***Aneityum***): *Bernardi 12927*, nr. Anawounamalo to R. Inwa Lelgey, 10-180 m, fl., yfr., 5 May 1968 (K, L, P); *Bernardi 12986*, nr. Anowounamalo towards Anitchavo (= Port Patrick), Ougaphaérek, Inréro, Ounétchnytap, to R. Inwa

Anetcho, 430 m?, fl., fr., 7-8 May 1968 (K, L, P); *Bernardi 13018*, ibid., 700 m, buds, 7-8 May 1968 (K, L, P); *Morrison s.n.*, s.loc., fr., 26 June 1896 (K); *Schmid 3558*, Sud, buds, Dec. 1970 (NOU).

LOCAL NAMES.—According to WHEATLEY (1992) names refer to the genus in general, e.g. Nomropom (Aneiteum), Nariop (Erromango), Aisensu (Paama), Kanumtep (Pentecost). Additional names from specimen labels include: Naruruturu (Efate), Owara (Fortsenale language, Santo), Nivlewi (Sie language, Erromango, meaning: drinking medicine [*Curry 550*]), Sasatré (Santo).

LOCAL USES.—The bark gives a red dye used on clubs (*Aubert de la Rüe s.n.*, 19 Dec. 1935). The wood is hard and durable and used for "hot" firewood and house construction (e.g. house posts and rafters) (WHEATLEY 1992; *Wheatley 207*). It is also used as medicine for asthma or "short wind" (*Curry 550*): the bark is stripped off and ground to a powder which is then put into a curled *Heliconia* leaf and cold water added; the leaf is squeezed and the extract drunk.

TYPIFICATION.—SEEMANN gave the type as "-Aneiteum, in woods (*M'Gillivray!*)". Sheets at K and BM lack a collector's name but bear the number 45. According to STAFLEU & COWAN (1985), SEEMANN's study set for the botany of the H.M.S. HERALD is at BM, but he published the names *Weinmannia denhamii* and *W. macgillivrayi* in his "Flora Vitiensis", for which K, and not BM, is considered to have the first set. Since the situation is somewhat confused, a lectotype is designated at K. The isolectotypes at P give both MACGILLIVRAY's name and the number 45. The date "Feb. 1859" is after MACGILLIVRAY had left the H.M.S. HERALD (DAVID 1995), and may refer either to when the material was received in London or when it was collected on a later expedition (see DAVID 1995: 218).

TAXONOMY AND VARIATION.—The leaves of *W. denhamii* are variable in both the number of pairs of leaflets and their shape. When there are few leaflets, they are usually lanceolate and when they are numerous, they are shorter and relatively broader. However, there is no discontinuity in the number of pairs of leaflets per leaf (R.D. HOOGLAND, unpublished, based on analysis of 38 sheets). Specimens with fewest leaflets are from Efaté, Santo and Anatom, and those with the most are from Tanna and Ambae.

BERNARDI (1964) placed *Weinmannia tannaensis* in sect. *Fasiculata* but the flowers are inserted singly and the inflorescence architecture is that of sect. *Leiospermum*.

IV. WEINMANNIA IN FIJI (with J.C. BRADFORD)

We recognize four species occurring in Fiji. In sect. *Fasciculata*, *Weinmannia richii* is endemic and relatively abundant on the two largest islands while *W. exigua* is known from Vanua Levu and also occurs in the Solomon Islands. In sect. *Leiospermum*, *W. vitiensis* is endemic and known only from three of the smaller islands and *W. affinis* is relatively abundant on Viti Levu, Taveuni and Ovalau, and has also been reported from Samoa although its status there is uncertain.

Key to the species in Fiji

1. Inflorescence a series of dyads or tetrads, the apical bud of the main stem present between the peduncles of the inner most partial inflorescences; lateral, auxiliary buds absent 2
1'. Inflorescence of triads or pentads, the apical bud of the main stem either developed into a partial inflorescence or aborted; lateral auxiliary buds present 3
2. Leaves on reproductive shoots usually trifoliolate, the terminal leaflet often much larger than the laterals .... **1. W. richii**
2'. Leaves on reproductive shoots usually imparipinnate with (1-)3-7 pairs of leaflets, the terminal leaflet not or scarcely larger than the largest laterals .... **2. W. exigua**
3. Leaves on reproductive shoots unifoliolate .... **3. W. affinis**
3'. Leaves on reproductive shoots usually trifoliolate, the rachis narrowly winged .... **4. W. vitiensis**

1. Weinmannia richii A. Gray

U.S. Expl. Exped., Phan. 1: 675, Atlas t. 85 (1854); Seem., Fl. Vit.: 110 (1865); Engl., Linnaea 36: 643 (1870), Nat. Pflanzenfam., ed. 2, 18a: 255 (1930); A.C. Sm., J. Arnold Arbor. 33: 133 (1952); Bernardi, Bot. Jahrb. Syst. 83: 177, t. 26 (1964); J. Parham, Pl. Fiji Islands: 124 (1972, rev. ed.); A.C. Sm., Fl. Vit. Nova 3: 20, fig. 5D (1985).—Type: *US 48071*, Fiji (Feejee) Islands, on mountains at Sandalwood Bay [= Mbua Bay *fide* Smith], Vanua Levu, 2000 ft., fr., 1840, US Expl. Exped. under the command of Capt. Wilkes (holo-, US 48071!; iso-, BM!, GH, K!, NY).

Weinmannia rhodogyne Gibbs, J. Linn. Soc., Bot. 39: 145 (1909); Engl., Nat. Pflanzenfam., ed. 2, 18a: 255 (1930).—Type: *Gibbs 594*, Fiji, Viti Levu, Nandarivatu, 2700 ft., fl., Aug. 1907 (holo-, BM!; iso-, K!).

Shrub or small tree 2-10(-20) m high. Branching not usually dichotomous. Nodes somewhat laterally flattened, the stipular scar arched on both sides, especially at distal nodes; internodes ca. 0.8-4.5(-8.5) cm. Young stems puberulent, older ones glabrous with numerous lenticels. Stipules caducous or not, suborbicular, up to 1.1 × 1.5 cm, rounded at apex, strigose to glabrous on abaxial surface. Leaves usually compound (1-)3(-7)-foliolate; total length up to 11 cm (for a trifoliolate leaf); petiole 0.9-1.5 cm long in trifoliolate leaves, to ca. 3 cm in imparipinnate ones; petiole and rachis segments where present subterete, slightly flattened or channelled on adaxial side, especially distally towards point of insertion of leaflets, scaly or puberulent; leaflets elliptical, rarely narrowly elliptical, lanceolate or ovate, often conduplicate when dry; in a trifoliolate leaf, lateral leaflets 2.1-5 × 0.7-3.9 cm, sessile, base ± equal to unequal, apex acute; apical leaflet often much larger than the laterals of the same leaf, 3.3-8.2(-9.5) × 1.1-3.2 (-4.4) cm, base attenuate, apex acute; in imparipinnate leaves, largest laterals about equal to terminal leaflet but not attenuate at base; blades subcoriaceous, glabrous, not punctate below; margin sometimes thickened, somewhat sinuate-crenate and undulate, ca. 8-12 crenations on each side of a leaflet; midrib slightly depressed above, prominent below and sparsely hairy, secondary and tertiary venation slightly raised on both surfaces.

Inflorescence usually (2-)4(-6) dyads or tetrads in a series at a node, sometimes a few successive nodes producing dyads or tetrads; peduncles 0.5-12 mm long, shortly strigose or with short erect hairs or almost glabrous; buds at most distal node of main stem and between the central pair of peduncles 1 or 3, sericeous; buds at apex of peduncle in angle between central pair of racemes sericeous, minute; rachises shortly pubescent, up to 10 cm long. Floral buds inserted in fascicles, tending to dissociate from the bract, the fascicles somewhat verticillate and the verticils somewhat separated so that sections of bare rachis visible between them; floral bracts about equal in length to buds, 1.5(-2) mm long, cymbiform, caducous, with short stiff hairs. Flowers unisexual or bisexual; pedicel 1-1.5 mm long, almost glabrous; calyx lobes 0.5-0.6 mm long, glabrous; petals obovate (not oblong) and often retuse at apex, 1-1.3 × 0.7-0.9 mm; disc lobes ca. 0.3 mm long; in female flowers: filaments 1-1.2 mm long, ovary pilose to densely pubescent, ca. 0.9 mm long, the styles ca. 0.9 mm long, ± straight or curved outwards; in male and bisexual flowers: filaments up to 2.2-3.8 mm, anthers ca. 0.4 mm long; in male flowers: ovary 0.4-0.5 mm long, the styles 0.4-0.5 mm long, curled inwards; in bisexual flowers (post anthesis): ovary ca. 1.1 mm long, the styles 1.1 mm long, straight or curved outwards.

Capsule 2-3.5 × 1.2-2 mm at dehiscence, the styles 0.5-1.5 mm, the exocarp almost smooth, softly pubescent; calyx lobes usually persistent; central column weakly developed, usually not persistent after valves have fallen. Seeds 0.8-1 mm long, 8 per capsule, comose at each end, the hairs to 1.5-2 mm long, much curled in capsule, later straight, sometimes with shorter hairs over the rest of the testa.—Fig. 9D-J, 10.

JUVENILE FOLIAGE.—*Hopkins & Bradford 5024*, sucker shoot in dense shade: leaves with up to 6 pairs of pinnae; leaflets chartaceous with serrate margins; stipules persistent, rounded and salverform, forming a horizontally flattened ring round the stem at nodes.

BREEDING SYSTEM.—Polygamodioecious.

FIELD CHARACTERS.—Shrub or small, compact tree with a dense, rounded or irregular crown.

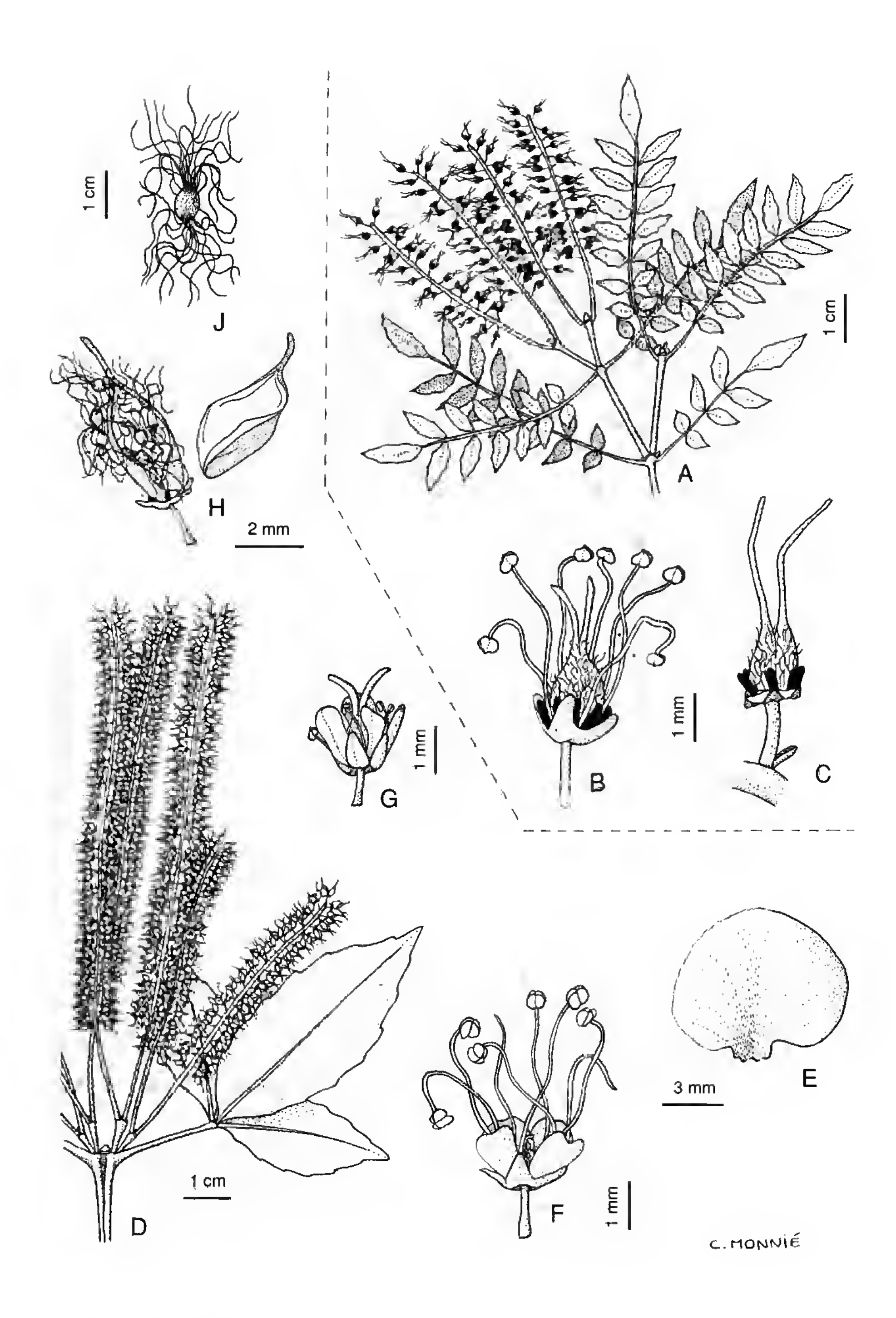


Fig. 9.—**A-C, *Weinmannia exigua***: **A**, shoot with infructescence of 2 dyads, the fruits immature; **B**, bisexual flower; **C**, immature fruit, note persistent bract at base of pedicel. (A-C, *Whitmore BSIP 995*).—**D-J, *Weinmannia richii***: **D**, shoot with infructescence of 4 dyads; **E**, stipule; **F**, male flower; **G**, female flower; **H**, dehisced capsule, one valve fallen and the other containing seeds; **J**, seed. (D, H, J, *Smith 6813*; E, *Gillespie 4333*; F, *Kuruvoli 16061*; G, *Gillespie 4233*).—Drawn by C. Monnié.

Flowers white, greenish white, creamy or somewhat pink and the pedicel pinkish; also recorded as yellow orange (TURRILL 1915).

DISTRIBUTION AND ECOLOGY.—Known from Viti Levu and Vanua Levu. Reported by BERNARDI from Samoa on the basis of sterile collections which are unlikely to be this species.

Occurring from 100-200 up to 1400 m, with the majority of records from 800-1000 m. Habitats include various types of forest (montane forest, ridge forest, open and dense forest [with tall gingers and tree ferns]) on ridges, slopes and in rolling country; also scrub and thickets in grassland and on dry slopes. Sometimes locally common. Field observations in central Viti Levu in March 1996 found that adult trees were often clumped and most were in fruit. There was a high degree of phenological synchrony both within individual trees and within populations (pers. obs.).

SELECTED COLLECTIONS (from a total of 32 studied).—FIJI: *Viti Levu*: *Damanu FD 991 D.177*, Serua, Naboutini, 1000 ft., buds, 21 Jan. 1964 (SUVA); *Degener 14379*, Tholo North, nr. Nandarivatu, Nandala fish hatchery, 750-900 m, fr., 4 Feb.-26 Mar. 1941 (A, BISH, K, L, P); *Gillespie 4233*, Tholo North prov., Nardarivatu, 2 miles along Nandran trail, 850 m, fl., 8 Dec. 1927 (BISH, GH); *Gillespie 4333*, Tholo North prov., slopes of Loma Langa Mt., 1100 m, fl., fr., 19 Dec. 1927 (BISH, GH); *Greenwood 384*, Lautoka, 600 ft., fr., 23 Oct. 1931 (A, K); nr. Monasavu Dam, 1 km N of FEA station, 840 m, fr., 28 Mar. 1996, *Hopkins & Bradford 5023* (MO, P, SUVA); *im Thurn 73*, Nandarivatu, fl., 1911 (BM, K, P); *Koroiveibau DA 11129*, Nailaga, Ba, buds, 19 Dec. 1957 (K, SUVA); *Kuruvoli DA 16061*, Macuata, Mt. Delainacau, fl., 9 Dec. 1968 (A, BISH, P, SUVA); *Parham DA 7121*, between Navai and Nadarivatu, Mba, Prov. Ba, 4340 ft., buds, fr., 15 Feb. 1951 (BISH, SUVA); *Qoro DA 12947*, Macuata, Tadradave, buds, 5 Nov. 1968 (SUVA); *Ranamu (DA) FD 1174*, Nadrao, Navosa, Nabosewale, Nadrau, 2700 ft., fl., 19 May 1967 (BISH, SUVA); *Smith 4710*, Nandronga, Navosa (formerly Tholo West), S slopes Nausori Highlands, Namosi Creek above Tumbenasolo, 300-450 m, fl., 29 May-5 June 1947 (A, BISH, L, P); *Smith 5739*, Mba, formerly Tholo North, W slopes of Mt. Nanggaranambuluta (Lomalangi), E of Nandarivatu, 850-1000 m, fr., 19 June-2 Oct. 1947 (A, BISH, K, L, P). *Vanua Levu*: *Parham DA 1122*, Bua or Mbua, Wairiki, fl., 1 May 1938 (A, SUVA); *Parham & Sealolo DA 2277*, Bua or Mbua, Ndama, 90 m, fr., 7 Dec. 1939 (A, SUVA); *Parham s.n.*, Bua Prov., fl., Jan. 1937 (A, BM); *Smith 6813*, Mathuata, Seanggangga Plateau, Korovuli R., nr. Natua, 100-200 m, fr., 25 Nov.-8 Dec. 1947 (K, L, P).

LOCAL NAMES.—Qalo (PARHAM 1941, sub *W. rhodogyne*); Manaui (*Parham DA 1122*); Vota (*Smith 6813*).

2. Weinmannia exigua A.C. Sm.

J. Arnold Arbor. 33: 137 (1952); Bernardi, Bot. Jahrb. Syst. 83: 166 (1964); J. Parham, Pl. Fiji Islands: 122 (1972, rev. ed.); A.C. Sm., Fl. Vit. Nova 3: 25, Fig. 5C (1985).—Type: *Horne 632*, Fiji, Vanua Levu, between Waiwai and Lomaloma, May 1878, fl., yfr. (holo-, K!).

Shrub or small tree, ca. 3-13 m high. Branching not usually dichotomous. Stems woody, not thickened at nodes and annular scar faint, internodes 0.5-2.3 cm long. Young stems minutely hairy, axillary buds densely hirsute, older stems glabrescent, bearing numerous pale lenticels. Stipules mostly caducous even in vegetative material, rarely seen, ± orbicular in outline with a narrowed base, ca. 0.5 × 0.5 cm, strigose on abaxial surface especially towards the base and glabrous on adaxial surface, margin somewhat recurved. Leaves usually imparipinnate, (1-)2-9 pairs of lateral leaflets, rarely unifoliolate, total length up to 5 cm long; petiole and rachis segments semiterete and very narrowly winged, the wings sometimes curved upwards to give a laterally compressed U-shaped cross section, often densely pubescent on adaxial surface along midrib, more sparsely hairy elsewhere, petiole up to 1 cm long (0.3 cm in unifoliolate leaves), rachis segments 0.3-0.5 cm long; lateral leaflets elliptical or sometimes obovate, the distal ones larger than the proximal ones (0.5-)1-1.7 × (0.3-) 0.4-0.6 cm, base acute and almost equal, apex acute; terminal leaflet narrowly elliptical, narrowly obovate to elliptical, 1.6-1 × 0.4-0.7 cm long, base attenuate, apex acute; blades glabrous except for midrib which is sparsely strigose below, coriaceous, not punctate; margin sometimes thickened, crenulate with 4-6 notches on each side in the lateral leaflets; midrib slightly depressed above and prominent below, secondary veins flat or very slightly raised above and below.

Inflorescence a pair of dyads or individual racemes, the apical bud of main stem densely velutinous, axillary buds at most distal leaf-bearing node often present and densely velutinous; bud at apex of peduncles between racemes minute, velutinous; peduncles 0.8-1 cm long, racemes up to 5 cm long; inflorescence axes sparsely hairy. Flowers inserted in fascicles; floral bracts caducous; female and bisexual flowers seen; pedicel ca. 1.5 mm long, minutely sparsely

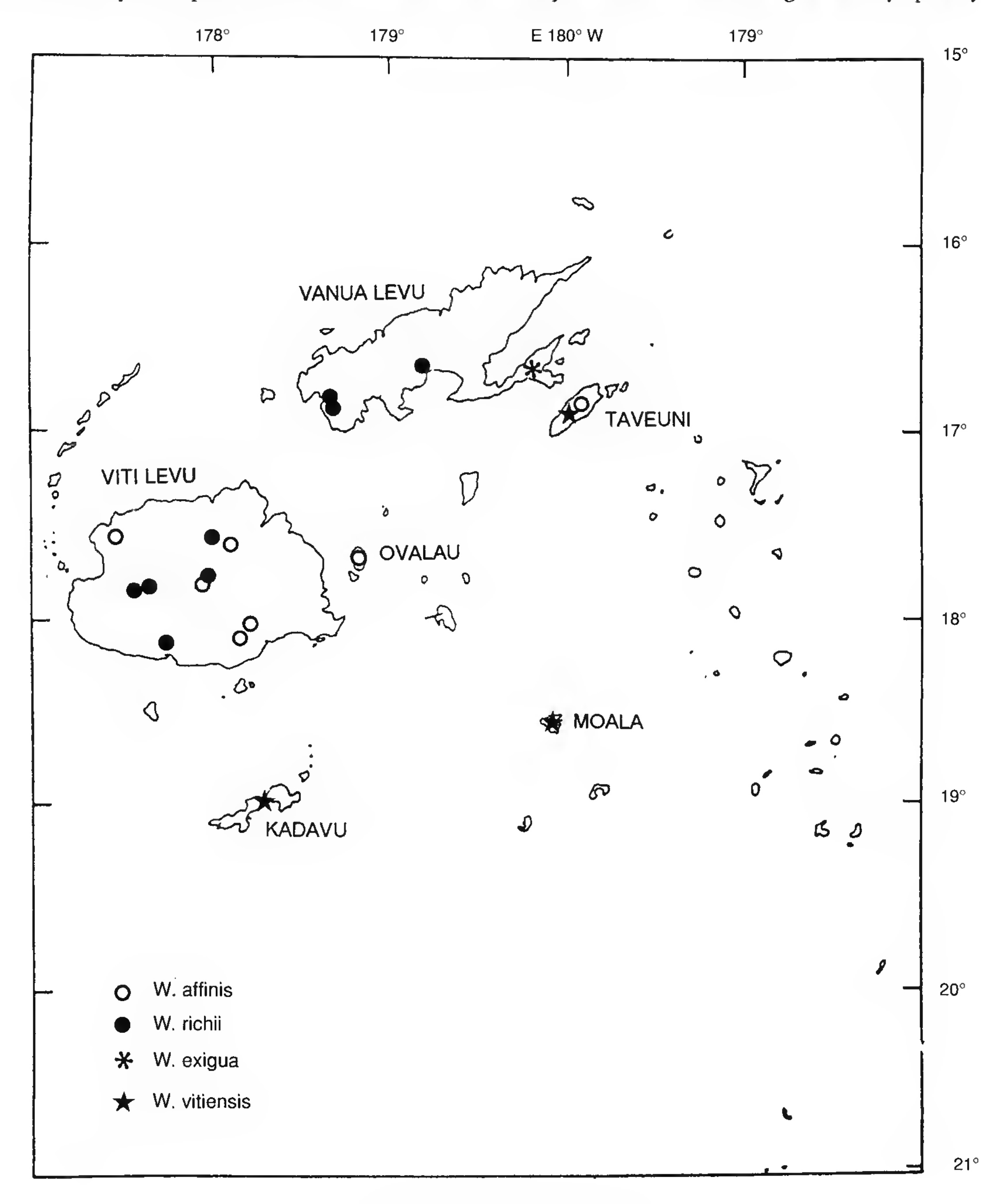


Fig. 10.—Distribution of ***Weinmannia*** in Fiji.

hairy; calyx lobes 0.6-0.7 mm long, glabrous; petals 1.1-1.4 × 0.6-0.7 mm, rounded or notched at apex; disc lobes 0.4-0.5 mm long; in female flowers: filaments ca. 1.3 mm and ovary ca. 1.3 mm long (but past anthesis), pubescent, with styles 1.2 mm long; in bisexual flowers: filaments ca. 4 mm long; ovary ca. 0.7 mm long at anthesis, densely velutinous, the styles 1.7-2 mm long. Immature fruit with ovary ca. 1.3 mm long, densely golden velutinous and styles ca. 2 mm long, glabrous, the calyx lobes mostly fallen, disc lobes persistent. Mature capsules and seeds not seen.—Fig. 5, 9A-C, 10.

BREEDING SYSTEM.—Polygamodioecious? *Horne 632* has female flowers and *Whitmore BSIP 995* (from the Solomon Islands) has bisexual ones.

FIELD CHARACTERS.—Habit appears to be variable as the type is described as a large shrub 10 ft. high, while in the Solomons it is a large tree.

DISTRIBUTION AND ECOLOGY.—Fiji (2 collections seen) and the Solomon Islands (1 collection seen). Habitats include high forest at 500-1000 ft. (*Howard 89*) and mountain top (*Horne 632*).

MATERIAL EXAMINED.—FIJI: ***Vanua Levu***: *Rangagone in Howard 89*, Thakaundrove, nr. tributary of Sovivi Creek, S of Karoko, Tunuloa District, Natewa Peninsula, st., May 1968 (BISH, K). Poorly collected but apparently common in montane forest.

Despite the wide disjunction, the leaves of the collections from the Solomons and Fiji are similar. *Weinmannia urdanetensis* also has numerous small leaflets and is the species which most resembles *W. exigua* but it differs in the details of the shape, texture and venation of the leaflets, and in the arrangement of the leaves. In the protologue, SMITH described the fruits and seeds but there are none on the type at K.

3. **Weinmannia affinis** A. Gray

U.S. Expl. Exped., Phan. 1: 674 (1854); Seem., Fl. Vit.: 110 (1865); Engl., Linnaea 36: 648 (1870), Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Reinecke, Bot. Jahrb. Syst. 25: 635 (1898); Gibbs, J. Linn. Soc. Bot. 39:145 (1909); Christoph., Bernice P. Bishop Mus. Bull. 154: 9 (1938), p.p.; A.C. Sm., J. Arnold Arbor. 33: 130 (1952); Bernardi, Bot. Jahrb. Syst. 83: 187, t. 30 (1964); J. Parham, Pl. Fiji Islands: 122 (1972, rev. ed.); A.C. Sm., Fl. Vit. Nova 3: 19, fig. 5A,B,E (1985).—Type: *US 48070*, Fiji (Feejee) Islands, on the mountains of Ovolau, 1200 ft., fr., U.S. Expl. Exped. under command of Capt. Wilkes (holo-, US 48070!; iso-, GH, K!, NY, P?).

Shrub or small compact tree 1-7 m high, rarely larger (20 m) or an epiphyte. Branching sometimes dichotomous (or into 4), the apical bud aborting, but not exclusively so; nodes somewhat thickened; glabrous except for young stems, inflorescence axes and pedicels shortly and sparsely strigose-pubescent, axillary buds sericeous, and ovary sometimes with short, sparse indumentum. Stipules variable in size, shape and persistence: either rhombic, obtrullate, ovate or broadly elliptical: either 0.5-1.1 × 0.35-0.6 cm and usually caducous when leaves small, or 1.1-1.9 × 0.6-1.6 cm, coriaceous and persistent, especially when leaves large; apex acute, almost round to cuspidate; margin sometimes toothed. Leaves simple, oblong, elliptical or broadly elliptical, the base decurrent into a short petiole 0.4-1.1(-1.6) cm long, the blade 1.8-9.8 × 1-4.8 cm, the apex acute to obtuse; punctate below; margin usually thickened, shallowly or markedly crenate or rarely sinuate, 9-14 notches down each margin of a leaf; midrib slightly raised above and prominent below, secondary and tertiary venation either flat, raised or obscure above and slightly raised below.

Inflorescence usually of 2 lateral triads or rarely 2 lateral pentads (central bud aborted), or sometimes 3 triads (central bud developed); further variants include four triads, developed from basal, lateral auxiliary buds, the central bud aborted; a few successive nodes of the main stem producing partial inflorescences simultaneously; peduncles 0.7-2.7 cm long; racemes usually short, 2.5-5 and not projecting beyond the foliage, rarely to 9 cm long; stipules at nodes within the inflorescence ligulate, sometimes persistent. Floral buds inserted singly; floral bracts not far exceeding length of buds, ligulate to cymbiform, ca. 0.7 cm long, not always fugaceous. Flowers unisexual or bisexual; pedicel 0.9-1.8 mm long;

calyx lobes 0.7-1.5 mm long; rarely pubescent; petals oblong or ovate, 1.2-1.8 × 0.9 mm; disc lobes 0.5-0.7 mm long; in male flowers: filaments up to 2.8-3 mm long, ovary ca. 1 mm long plus styles of 0.2 mm; in female flowers: filaments ca. 1 mm long; ovary (past anthesis) ca. 2 mm long plus styles 1.1 mm long.

Capsules 2.2-3.8 × 1.3-2.2 mm at dehiscence, the styles 1-1.3 mm long, the exocarp somewhat longitudinally ridged, glabrous or sparsely strigose-pubescent; calyx lobes caducous; free central column present. Seeds ca. 0.9 mm long, comose at both ends.—Fig. 10, 11A-F.

JUVENILE FOLIAGE.—*Hopkins & Bradford 5038*, 1 m high sapling: leaves 3-5 foliolate; leaflets chartaceous with serrate margin; stems, leaf rachis and underside of the midrib pubescent; stipules large, persistent, toothed. Small shrubs in open, disturbed areas had leaves relatively far down the stems, the lower ones usually trifoliolate and upper ones simple, sometimes with long internodes (ca. 10 cm).

BREEDING SYSTEM.—Polygamodioecious.

FIELD CHARACTERS.—Densely branched shrub or small compact tree 1-7(-20?) m high. Flowers white, the calyx and ovary pale green or white; petals and filaments white, stigmas tinged purple; disc lobes dark red and strongly contrasting with pale corolla; anthers pink or cream. Female inflorescences are comparatively small and inconspicuous, scarcely projecting beyond the foliage while male inflorescences are longer and exserted beyond the leaves (J.C. BRADFORD pers. obs.).

DISTRIBUTION AND ECOLOGY.—Highland regions of Viti Levu, Taveuni and Ovalau; also reported from Samoa. Recorded from dry open forest, dense ridge scrub and windswept thickets on mountain summit, escarpment edge and swamp, at (360-)700-1410 m on Viti Levu, 840-1100 m on Taveuni and 500-600 m on Ovalau. Common on summit of Mt. Victoria (Tomanivi). The form with large persistent stipules occurs in the Namosi District of Viti Levu and on Ovalau.

In March 1996 we found this species at three localities, always on the highest peaks and ridges in the vicinity and sometimes in boggy areas. Near Monasavu Dam, Viti Levu, in disturbed forest its associates included *Pullea glabra* and *Spiraeanthemum serratum* (Cunoniaceae), *Rubus*, *Vaccinium*, Melastomataceae, Zingiberaceae, *Lycopodium*, tree ferns and Gleicheniaceae (see *Hopkins & Bradford 5021*). On the summit of Des Voeux Peak, Taveuni, sterile shrubs 1-3 m high were one of the dominant components of disturbed areas near the telecom tower (*Hopkins & Bradford 5035*, *5039*) with *Scaevola floribunda*. It was also relatively common in undisturbed cloud forest with abundant *Freycinetia* along the ridge towards Lake Tagimaucia. *Weinmannia affinis* showed less synchrony in its reproductive behaviour than *W. richii*. Both within populations and within individuals we observed inflorescences at several stages of development including mature flowers.

Where *W. affinis* occurs at the same locality as other *Weinmannia* species, there appears to be some ecological separation between them. For instance, near Monasavu Dam, *W. affinis* was found as a small tree or shrub in fairly short forest near the road at its highest elevations (1070-1210 m) and *W. richii* was seen as a 20 m high tree in taller forest at lower elevation (ca. 840 m) in the same general area. On Des Voeux Peak, Tavenui, *W. affinis* was again found only near the summit and along ridges (ca. 1100 m) as a small tree, shrub or epiphyte while mature trees of *W. vitiensis* were only seen below 900 m in taller forest on the mountain slope.

SELECTED COLLECTIONS (from a total of 30 studied).—FIJI: ***Viti Levu***: *Bradford 591*, Tomanivi (Mt. Victoria), trail from Navai to ridge crest below summit, 17°38'S-178°01'E, fl., 30 Mar. 1996 (MO, P, SUVA); *Gibbs 642*, Nadarivatu, 2700 ft., fl., Sep. 1907 (BISH, BM, K); *Hopkins & Bradford 5022*, nr. Monasavu Dam, road S from dam, 1210 m, fl., 29 Mar. 1996 (MO, P, SUVA); *Koroiveibau DA 14184*, Ba, Mt. Evans Range, Natualevu, 3000 ft., fl., 8 Apr. 1965 (BISH, SUVA); *Koroiveibau & Qoro DA 14574*, Namosi, Mt. Nadobe, 2825 ft., fl., 16 Nov. 1965 (GH, L, SUVA); *Koroiveibau DA 14702*, Namosi, Mt. Vakarogosiu, summit, 3400 ft., fr., 23 Nov. 1965 (K, SUVA); *Kuruvoli DA 13890*, Nausori Highlands, 1900 ft., fr., 20 July 1964 (K, SUVA); *Parham DA 2201*, Namosi, Korobasabasaga, summit, 3950 ft., fl., 24 Mar. 1940 (A, BISH, SUVA); *Parham DA 2598 pro parte*, Namosi, Voma Peak, 2000 or 3000 ft., fl., 23 June 1939 (A, BISH, SUVA); *Smith 4905*, Mba

(formerly Tholo North), nr. Nandarivatu, 800-900 m, fr., 26 June-19 Oct. 1947 (A, BISH, K, L, P); *Thomerson DA 19527*, Nandronga-Navosa, Nausori Highlands, 850 m, fl., 29 Oct. 1985 (SUVA); *Webster & Hildreth 14204*, Mba, Tuvua, summit Mt. Victoria (Tomanivi), 4300 ft., fr., 13 July 1968 (GH, SUVA). ***Taveuni***: *J. & W. Ash DA 19957*, Lake Tagimaucia, Somosomo, 850 m, fr., 15 Sep. 1982 (SUVA); *Hopkins & Bradford 5036*, Des Voeux Peak, nr. telecom tower and ridge towards crater & lake, 1000-1100 m, buds, 2 Apr. 1996 (MO, P, SUVA); *Seemann 200*, Vuna (fide Smith), fr., 1860 (BM, GH, K, P); *Smith 878*, borders of Lake E of Somosomo, 700-900 m, fr., 29 Dec. 1933-8 Jan. 1934 (BISH, K). ***Ovalau***: *Smith 7608*, summit Mt. Ndelaiovalau, 575-626 m, fr., 11-25 May 1953 (BISH, GH, K, L, P, SUVA); *Smith 7704*, summit Mt. Tana Lailai, 500-550 m, fl., 1 June 1953 (BISH, GH, L, P, SUVA).

LOCAL NAMES.—Katakata (*Smith 4905*); Vure (*Gillespie 2736*).

VARIATION.—The size of the leaves and the size and persistence of the stipules are variable but the material cannot be readily divided into more than one taxon (see SMITH 1985). The majority of collections have small or medium sized, ± coriaceous leaves and small, caducous stipules (Fig. 11B). A few collections have larger leaves and some of these have large, persistent stipules that are rounded or pointed at the apex (Fig. 11A,C), e.g. *Smith 7608* from Ovalau, *Parham DA 2598 pro parte* and *Koroiveibau DA 14702* from Namosi region, Viti Levu.

4. Weinmannia vitiensis Seem.

Fl. Vit.: 110 (1866); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); A.C. Sm., J. Arnold Arbor. 33: 135 (1952); Bernardi, Bot. Jahrb. Syst. 83: 207, t. 38 (1964); J. Parham, Pl. Fiji Islands: 125 (1972, rev. ed.); A.C. Sm., Fl. Vit. Nova 3: 22 (1985).—Type: *Seemann 199*, Fiji, Kadavu (holo-, K!, photo US!; iso-, BM!, P!, also G, GH, MEL, NSW *fide* HOOGLAND).

Shrub or tree 3-20 m high. Branching often dichotomous. Stems woody, somewhat thickened at nodes, annular scar visible, internodes ca. 0.7-3 cm long. Young stems minutely or sparsely strigose, older stems glabrous with numerous prominent lenticels, axillary buds densely velutinous, acute at apex. Stipules fugaceous even in vegetative material, ligulate to shortly spathulate, apex rounded to acute, to 3 mm long, minutely hairy to ± glabrous. Leaves usually trifoliolate, rarely simple, total length up to 8 cm including petiole of 0.9-2 cm; petiole semiterete and narrowly winged, especially distally, midrib prominent above, glabrous; lateral leaflets elliptical (2.1-)3.3-4.7 × (0.8-)1-1.6 cm, unequal at base, acute at apex; terminal leaflet elliptical or sometimes narrowly obovate, often larger and broader than the laterals, 4.3-6.5 × 1.3-2 cm, base attenuate, apex acute; leaflet blades glabrous, coriaceous, punctate below; margin sometimes thickened, crenate, the crenations acroscopic, 11-13 on each side of a leaflet; midrib slightly raised above and prominent below, secondary and tertiary venation slightly raised on both surfaces, often drying paler than intervenium.

Inflorescence a central triad or pentad with the lower racemes either in axils of leaves or not, or in the axils of reduced leaves, sometimes also with a pair of lateral triads; sometimes a few successive nodes on a shoot producing partial inflorescences simultaneously; lateral auxiliary buds sometimes present at lower nodes of inflorescence; peduncle and rachis segments 0.7-1.3 cm long, sparsely pubescent, racemes 4-7 cm long. Floral buds inserted singly; floral bracts to 1 mm, cymbiform or dagger-shaped, almost glabrous, caducous. Flowers unisexual; pedicel 0.2-3 mm long, almost glabrous; calyx lobes 0.6-0.8 mm long, glabrous; petals 0.9-1.5 mm long; disc lobes 0.3-0.8 mm long; in male flowers: filaments 2-2.5 mm long, the anthers 0.5 mm long and ovary ca. 1 mm long, glabrous, the styles 0.2-0.3 mm long; in female flowers: the filaments to ca. 0.7 mm, ovary (post anthesis) 1.1-1.5 mm long, sparsely strigose, the styles ca. 0.5 mm long.

Capsules 1.8-2.5 × 0.9 mm at dehiscence, the styles 0.5 mm or less long, the exocarp sparsely strigose, with minute longitudinal ridges, calyx lobes not persistent, central column present. Seeds ca. 0.7 mm long, ca. 16 per capsule, comose at both ends.—Fig. 10, 11G-K.

JUVENILE FOLIAGE.—Differs markedly from adult: see *Hopkins & Bradford 5042*, from a sapling 3.5 m tall growing in shade, Taveuni:

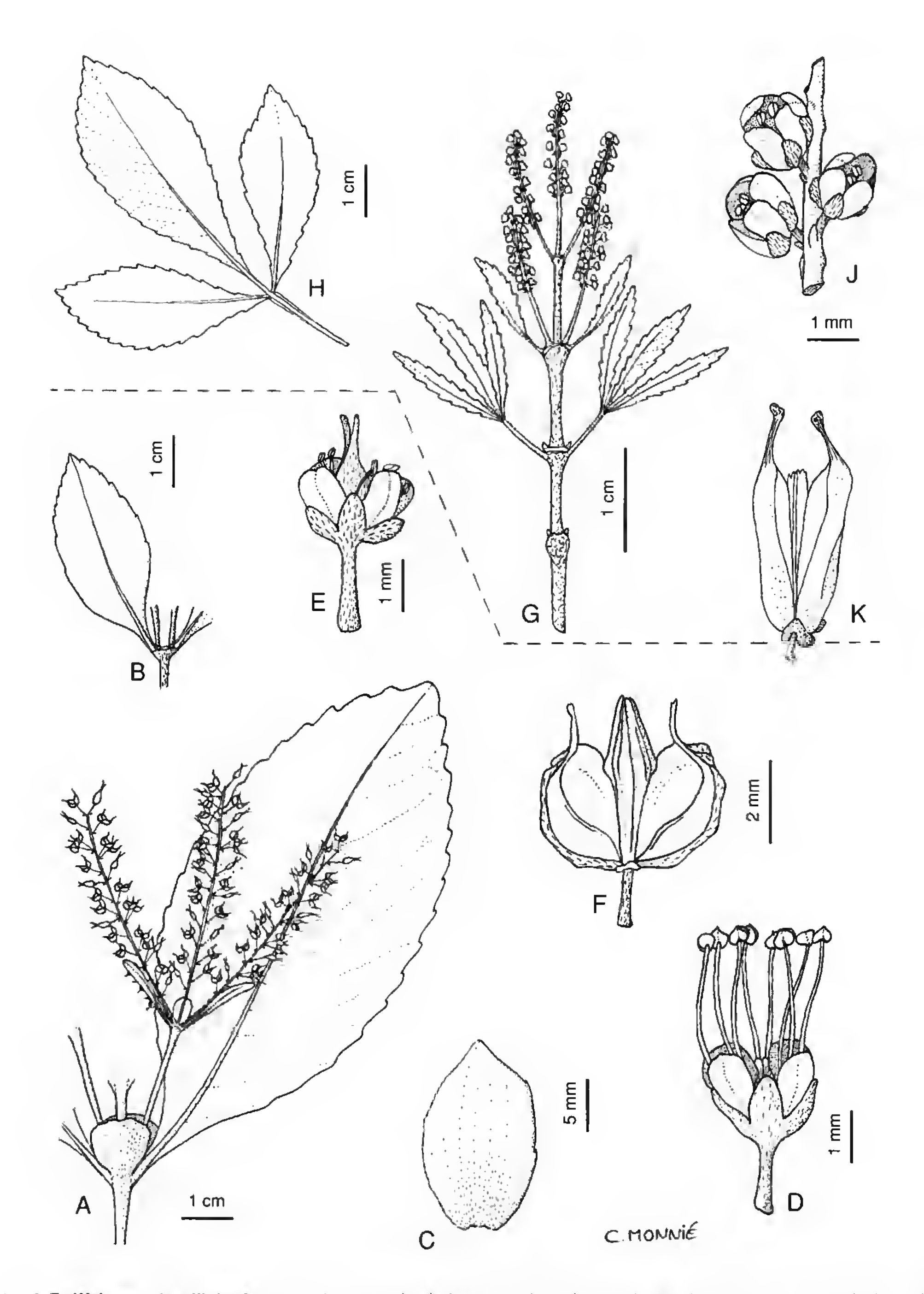


Fig. 11.—**A-F**, ***Weinmannia affinis***: **A**, shoot with large simple leaves and persistent stipules; infructescence a triad with reduced leaves at node; **B**, shoot with small simple leaves, the stipules caducous; **C**, stipule from A; **D**, male flower; E, female flower; **F**, dehisced capsule. (A, C, F, *Smith 7606*; B, *Seemann 200*; D, *Gibbs 642*; E, *Parham 2201*).—**G-K**, ***Weinmannia vitiensis***: **G**, shoot with an immature inflorescence (pentad) and reduced leaves at two nodes; **H**, leaf with slightly winged petiole; **J**, section of inflorescence axis showing flower buds inserted singly; **K**, dehisced capsule. (G-K, *Bryan 317*).—Drawn by C. MONNIÉ.

leaves imparipinnate with 2-4 pairs of leaflets; leaflet margins crenate; petioles terete (not winged) with dense, erect hairs; stipules large, almost round, toothed.

BREEDING SYSTEM.—Dioecious. Flowers unisexual but little material is available.

FIELD CHARACTERS.—Dense shrub or tall, canopy tree, sometimes gnarled. Bark rough, scaly, light grey; sapwood orange-brown, coarse; heartwood yellow-brown, moderately hard. Flowers white with a slight fragrance; pedicel and calyx pale green, corolla and filaments white, anthers cream, disc lobes dark brown-red.

DISTRIBUTION AND ECOLOGY.—Known only from three of the smaller Fijian high islands at 300-900 m. Habitats include tall, dense forest on mountain slope (*Hopkins & Bradford 5041*), and forest on summit ridge (*Bryan 317*); also in open areas among bracken; locally frequent.

MATERIAL EXAMINED.—FIJI: ***Kadavu***: *Seemann 199*, buds, 1860 (BM, K, P), type. ***Taveuni***: *Hopkins & Bradford 5041*, Des Voeux Peak, W side, 900 m, fl., 2 Apr. 1996 (MO, P, SUVA); *Smith 8401*, hills E of Somosomo, W of old crater, 660-900 m, st., 18 Aug. 1953 (BISH, GH, K, L, P, SUVA). ***Moala***: *Bryan 317*, summit ridge, 300 m, buds, fr., 11 July 1924 (BISH, K); *Smith 1354*, Ndelaimoala, fr., 20-24 Mar. 1934 (BISH, K, P); *Harvey s.n.*, Feegee (sic) Islands, s.loc., Nov. 1855 (K).

LOCAL NAME.—Molau ndamu (*Smith 1354*).

RELATIONSHIPS.—Regarded by SMITH (1985) as not sharply distinct from *Weinmannia richii*, but the structure of the racemes and the inflorescences are quite different and these species belong to different sections of the genus. On present evidence there is no overlap in the distributions of *W. vitiensis* and *W. richii*.

Besides the differences in the leaves and habitat between *Weinmannia vitiensis* and *W. affinis*, in the former the apical buds of the shoots abort less often so that dichotomous branching is less frequent.

BERNARDI (1964) included *Weinmannia raiateensis* J.W. Moore (from Raiatea, Society Islands) in *W. vitiensis*. Both have trifoliolate leaves with a narrowly winged rachis; the leaves of *W. raiateensis*, however, tend to be smaller and less coriaceous than those of *W. vitiensis*.

Doubtful species

Weinmannia spiraeoides A. Gray

U.S. Expl. Exped., Phan. 1: 677 (1854); Seem., Fl. Vit.: 110 (1865), Engl., Linnaea 36: 644 (1870), Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); A.C. Sm., J. Arnold Arbor. 33: 133 (1952); Bernardi, Bot. Jahrb. Syst. 83: 208 (1964); J. Parham, Pl. Fiji Islands: 125 (1972, rev. ed.); A.C. Sm., Fl. Vit. Nov. 3: 20 (1985).—Type: *US 48073*, Fiji (Feejee) Islands, Ovolau, U.S. Expl. Exped. under the command of Capt. Wilkes (holo-, US 48073!).

Known only from the sterile type which has chartaceous, 3-5-foliolate leaves with dentate margins and toothed stipules. It appears to be juvenile foliage of *Weinmannia* as suggested by SMITH (1985). However, immature foliage is so variable as to preclude identification in most cases (see HOPKINS 1998a). It is unlikely that this name represents a distinct taxon.

V. WEINMANNIA IN SAMOA AND THE COOK ISLANDS

Weinmannia has been collected from Savai'i and 'Upolu in Western Samoa and from Tutuila and the Manua group (Ta'u and Olosega) in American Samoa. It also occurs on Rarotonga in the Cook Islands to the SE but is not known from Tonga or Niue. Three species have been described fom this region: *W. samoensis* A. Gray, *W. manuana* Christoph., and *W. rarotongensis* Hemsl. in Cheeseman (HOPKINS & FLORENCE 1998, Fig. 7F-M); all belonging to sect. *Leiospermum*. *Weinmannia affinis* and *W. richii* from Fiji have also been reported (CHRISTOPHERSEN 1938; BERNARDI 1964).

Three treatments of *Weinmannia* have been published for this region, none of them satisfactory. CHRISTOPHERSEN (1938) recognised four species: *W. manuana*, *W. affinis*, *W. richii* and *W. samoensis* and did not discuss *W. rarotongensis*. SMITH (1952) considered all the species in Samoa to be endemic and recognised *W. samoensis*, *W. manuana* and *Weinmannia sp.* (based on *Christophersen 787*, *2561*, *2735*, all sterile); *Christophersen 534* (also sterile) was

unplaced; *W. rarotongensis* was separated from *W. samoensis* by implication. BERNARDI (1964) placed *W. manuana* into synonomy with *W. affinis*, included *W. rarotongensis* in *W. samoensis*, and recognised *W. richii*, based on *Christophersen 534, 787* and *Rechinger 1647*. Thus none of his species was endemic to Samoa.

A. WHISTLER (pers. comm.) and J.C. BRADFORD (pers. comm.) have seen *Weinmannia* growing in Samoa, and both consider that there is only a single, variable species in this group of islands, whose leaves can therefore be unifoliolate, trifoliolate or imparipinnate. BRADFORD (pers. comm.) found that at lower elevations, trees usually had 3-7 leaflets per leaf and at higher elevations, 1-3 leaflets per leaf.

From studies of herbarium specimens, I have failed to reach a conclusion about the taxonomy of species from Samoa and the Cook Islands, and to avoid making matters worse, will comment only on the possible occurrence of the Fijian species. All the trifoliolate collections I have seen from Samoa referred by BERNARDI and CHRISTOPHERSEN to *Weinmannia richii* are sterile and likely to be juvenile specimens of other taxa. I have seen no fertile material from Samoa which could be equated with *W. richii*, which should therefore be considered endemic to Fiji. Several specimens with small, unifoliolate leaves from Samoa cannot be separated from *W. affinis* although many of the unifoliolate collections fall outside the range of the Fijian material. It is thus not clear at present whether *W. affinis* is endemic to Fiji or not.

The structure of the inflorescence of all collections seen from Samoa and Rarotonga is typical for sect. *Leiospermum*.

VI. WEINMANNIA IN NEW CALEDONIA (with R.D. HOOGLAND†)

Four endemic species of *Weinmannia* occur in New Caledonia (HOOGLAND, unpublished manuscript at P). Full synonomy, descriptions and citation of specimens will be published in the "Flore de la Nouvelle-Calédonie" and only a summary is given here. The taxonomic changes indicated here should be attributed to HOOGLAND, and in the citation of types below, ! shows that a specimen has been seen by him.

All the species in New Caledonia belong to sect. *Leiospermum* and appear more closely related to one another than to other members of the section. They have small, caducous, usually ligulate stipules in mature foliage; juvenile foliage may have more persistent, salverform stipules. The flowers are bisexual and white, and the calyx lobes usually fall in fruit. In *Weinmannia dichotoma*, *W. paitensis* and *W. ouaiemensis*, vegetative growth often involves dichotomous branching, and in the inflorescence, the apical bud is often aborted. When this is not so, the apical and axillary buds usually develop equally. Lateral auxiliary buds are especially prominent in the inflorescences of *W. dichotoma* (see HOPKINS 1998a, Fig. 3M).

Key to the species of New Caledonia

1. Leaves on reproductive branches always simple .... **2. W. paitensis**
1'. Leaves on reproductive branches trifoliolate 2
2. Vegetative growth usually by development of both apical and axillary buds, i.e. branching not dichotomous; inflorescence usually a central, apical triad (or sometimes a penrad), often with two lateral triads .... **1. W. serrata**
2'. Vegetative growth almost exclusively by development of shoots from lateral, axillary buds, the apical bud aborted, i.e. branching dichotomous, though the branches sometimes unequal; inflorescence usually a pair of lateral dyads or triads, the apical bud aborted (rarely otherwise) 3
3. Young shoots sparsely hairy to glabrescent; upper surface of leaflets glabrous; pedicel 0.3-0.5 mm diameter, glabrous or briefly and sparsely hirsute; filaments 2.5-4.5 mm long; ovary sparsely strigose with 8-12 (-14) ovules per locule; styles 2-3 mm long .... **3. W. dichotoma**
3'. Young shoots and inflorescence axes densely tomentose; upper surface of leaflets loosely hirsute, glabrescent; pedicel 0.5-0.7 mm diameter, moderately hirsute; filaments 5.5-6 mm long; ovary strigose-hirsute with 12-16 ovules per locule; styles 2-3 mm .... **4. W. ouaiemensis**

1. Weinmannia serrata Brongn. & Gris

Bull. Soc. Bot. France 9: 73 (1862).—Type: *Vieillard 572*, Hab. in montibus Novae Caledoniae, prope Balade (holo-, P!; iso-, NSW!).

Vegetative branching often dichotomous. Leaves subcoriaceous, not punctate below. Inflorescence usually a central triad or pentad, often with lateral triads developing from axillary buds (i.e. apical bud reproductive, rarely aborted); reduced leaves sometimes present at nodes within the inflorescence.

Tree up to 25 m, widespread on Grande Terre in humid forest and gallery forest between 150-800 m, on greywackes, schist and basalt.—Fig. 12A-E.

2. Weinmannia paitensis Schltr.

Bot. Jahrb. Syst. 39: 124 (1906).—Type: *Schlechter 14941*, New Caledonia, Sud-Bezirk: auf dem Gipfel des Mont Mou bei Paita, ca. 1250 m (holo-, B; iso-, BM, BR, E, G, K, L!, LAU, LE, M, NSW!, P!, W, Z! *fide* BERNARDI and HOOGLAND).

Weinmannia ?thornei Guillaumin in Guillaumin et al., Stud. Nat. Hist. Iowa Univ. 20: 31 (1965).—Type: *Thorne 28733*, New Caledonia, Mt. Mou, 1050 m, 8 Nov. 1959 (holo-, P!; iso-, L!, P!, RSA, Z); *syn. nov.* of HOOGLAND.

Vegetative branching usually dichotomous; dichotomous branching is fixed in juvenile plants while in adult foliage, branching can be dichotomous or not (J.C. BRADFORD pers. comm.). Leaves on reproductive shoots simple but foliage on lower branches within the crown trifoliolate. Leaves coriaceous, often punctate below. Inflorescence a pair of lateral dyads or triads, the apical bud aborted; dyads without buds between the racemes.—Fig. 12F-H.

A small tree known from Mt. l'Aoupiné and several mountains towards the south, including Mt. To, Mt. Kouakoué, Mt. Ouin and Mt. Mou, in dense humid forest from (500-)950-1300 m, on ultrabasic or schistose rocks.

3. Weinmannia dichotoma Brongn. & Gris

Bull. Soc. Bot. France 9: 73 (1862).—Type: *Vieillard 569*, Hab. in montibus Novae Caledoniae, prope Balade (lecto- of BERNARDI, P!; isolecto-, P!).

Weinmannia monticola Däniker, Vierteljahrsschr. Naturf. Ges. Zürich 76 = Mitt. Bot. Mus. Zürich 137: 165 (1931).—Type: *Däniker 1812*, New Caledonia, auf den flanchen Hohenrucken an der Westflanke des Ignambi, 6 June 1925 (holo-, Z!); *syn. nov.* of HOOGLAND.

Vegetative branching largely dichotomous. Leaves on reproductive shoots trifoliolate, those on lower leaves and immature foliage 3-7-foliolate. Leaves coriaceous, often punctate below. Inflorescence a pair of dyads or sometimes triads in larger-leafleted specimens, the apical bud aborted. Auxiliary buds at base of peduncle, in a plane perpendicular to that of the leaf-bases, large and conical.

Shrub or small tree up to 12 m. Widespread on Grande Terre in humid forest on mica-schist at 400-1550 m and ultrabasic substrate between 950 and 1300 m.

BERNARDI (1964) regarded *W. monticola*, with larger leaflets, as distinct from *W. dichotoma* but there are numerous intermediates. The possibility of any ecological differences correlated with leaflet size needs to be investigated in the field.

On Mt. Mou, the shape of the leaves approaches that of *W. serrata*, with a fairly sinuate margin. On both Mt. Ouin and Mt. Mou it grows in close proximity to *W. paitensis* in *Nothofagus* cloud forest on deep, peaty soil (BRADFORD & HOPKINS pers. obs.). The immature foliage of these two species can be difficult to separate although mature canopy foliage is clearly distinct.

4. Weinmannia ouaiemensis
(Guillaumin & Virot) Hoogland, **comb. nov.**

Cunonia ouaiemensis Guillaumin & Virot, Mém. Mus. Natl. Hist. Nat., sér. B, Bot. 4: 28 (1953).—Type: *Virot 731*, New Caledonia, Arête rocheuse menant au Mt. Mi (versant W) point culminant du massif de la Roche Ouaième, 1050 m (holo-, P!; iso-, A, P! 2 sheets).

Vegetative branching dichotomous. Leaves trifoliolate, the petiole not winged; blade coriaceous, punctate below, the margin revolute; white

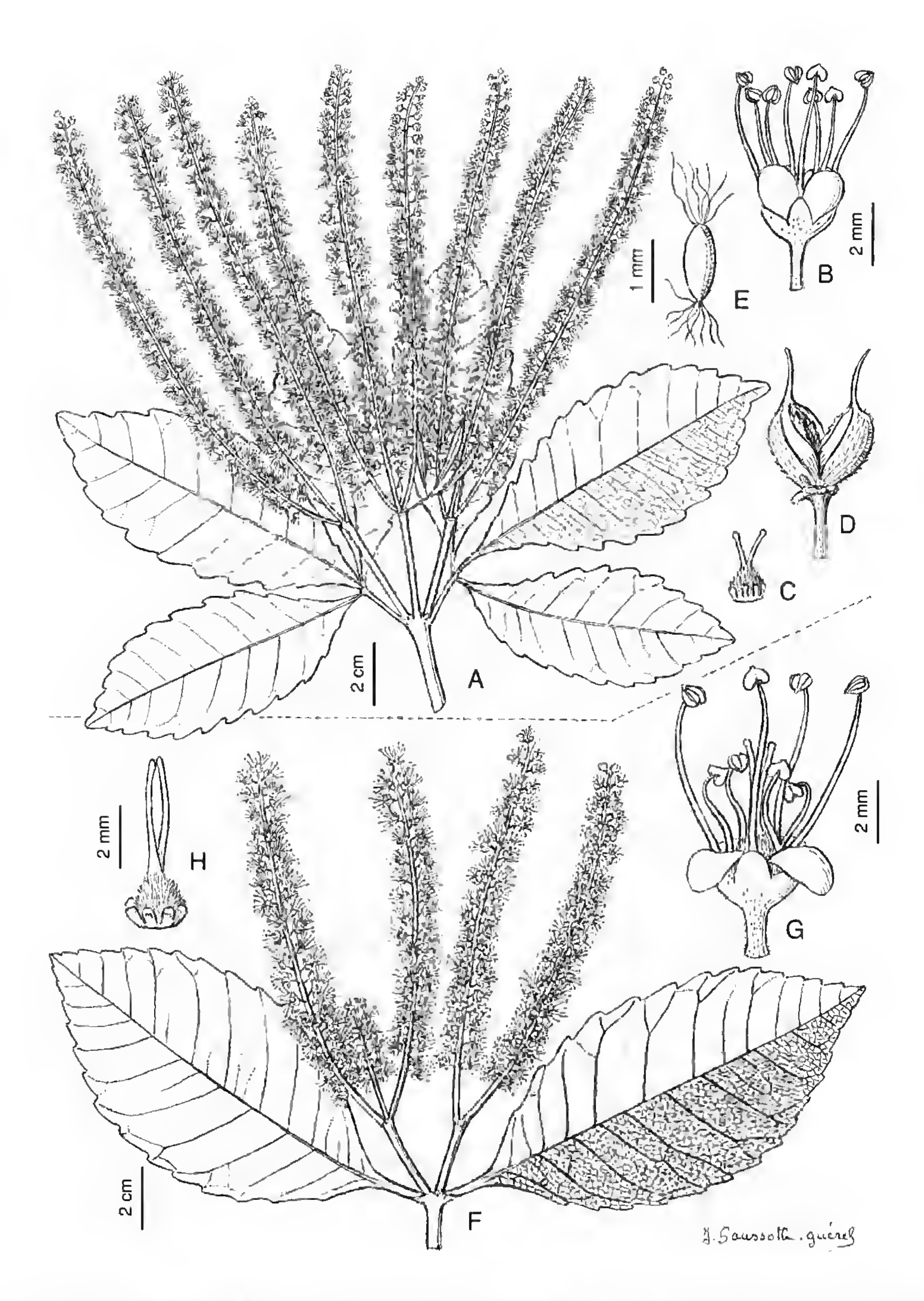


Fig. 12.—**A-E**, ***Weinmannia serrata***: **A**, flowering shoot with an inflorescence of three triads; one triad has an reduced leaf at the node where the racemes arise; note small auxiliary buds at base of lateral triads; **B**, bisexual flower at anthesis; **C**, gynoecium and disc lobes; **D**, dehisced fruit; **E**, seed. (A-C, *MacKee 25614*; D, E, *MacKee 18445*).—**F-H**, ***Weinmannia paitensis***: **F**, flowering shoot with an inflorescence of one triad and one dyad, the apical bud aborted; **G**, bisexual flower at anthesis; **H**, gynoecium and disc lobes. (F-H, *Thorne 28733*).—Drawn by J. Saussotte-Guérel.

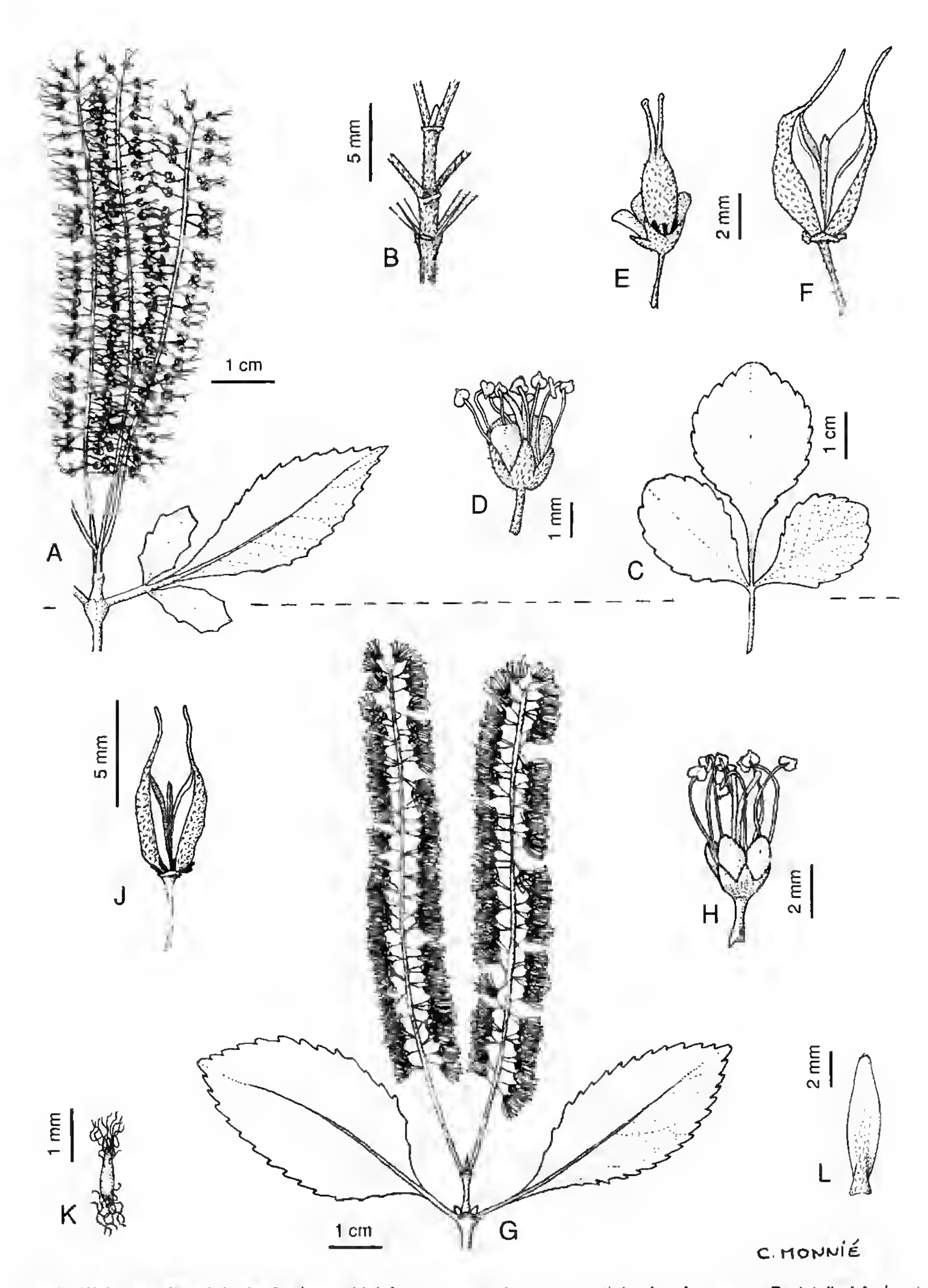


Fig. 13.—**A-F, *Weinmannia sylvicola***: **A**, shoot with infructescence of two sequential pairs of racemes; **B**, detail of A showing bases of opposite petioles at lowest node, bases of opposite and decussate racemes at subsequent nodes and dormant apical bud; **C**, trifoliolate leaf; **D**, bisexual flower; **E**, immature fruit; **F**, capsule at dehiscence. (A, B, D, E, *Hynes s.n.*, 10 Feb. 1952; C, *Colenso s.n.*; F, *van Steenis 22314*).—**G-K, *Weinmannia racemosa***: **G**, flowering shoot (inflorescence a median dyad with a dormant apical bud); **H**, bisexual flower; **J**, capsule at dehiscence; **K**, seed; **L**, stipule. (G, H, *Varekamp 97*; J, K, *Lam 7083*; L, *van Zaten 1331*).—Drawn by C. MONNIÉ.

deposit on upper surface of old leaves. Inflorescence a pair of lateral dyads (without a bud between the racemes) or triads, the apical bud usually aborted or rarely developed into a dyad.

Stunted shrubs endemic to Roche Ouaième, in exposed thicket and low humid forest on mica-schist, between 700-1150 m.

VII. WEINMANNIA IN NEW ZEALAND

There are two closely related allopatric species occurring in New Zealand: *Weinmannia racemosa* L. f. occurs on South and North Islands, as far north as Hamilton, and *W. sylvicola* Sol. ex A. Cunn. is found on North Island, to the north of Hamilton (BERNARDI 1964; WARDLE 1966). These two species appear to be closely related and are superficially similar to one another, but the adult leaves of *W. racemosa* are usually simple (Fig. 13G) while those of *W. sylvicola* are usually trifoliolate (Fig. 13A,C) (and see WARDLE for further differences).

In both species the flowers are inserted singly in the axils of bracts on the racemes, as in other species of sect. *Leiospermum*. Other characrers that they share with most species of this section are: leaves often punctate below; leaf rachis slightly expanded; stipules caducous and where present, ligulate not orbicular (Fig. 13L); calyx lobes fallen in fruit (Fig. 13F,J) (a few exceptions); calyx lobes glabrous or sparsely strigose. These species also show a number of features which are not widespread within the section. The flowers are somewhat perigynous (Fig. 13E) (rather than hypogynous), and they may have a greater tendency to be 5-merous or to have a 3-merous ovary than other Pacific species. The flowers are bisexual (Fig. 13D,H), as in the New Caledonian species, where as in most Pacific species the majority of inflorescences have unisexual flowers. The inflorescences differ somewhat from those of other Pacific species and are described by HOPKINS & BRADFORD (HOPKINS 1998a).

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A revision of *Weinmannia* (Cunoniaceae) in Malesia and the Pacific. 4. The Society, Marquesas and Austral Islands

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KEY WORDS
Weinmannia,
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Society Islands,
Marquesas Islands,
Rapa Island.

ABSTRACT
Six species are recognized in this region, all belonging to sect. *Leiospermum*. *Weinmannia rapensis* is confined to Rapa in the Austral Islands and its reported occurrence in Pitcairn is discussed. *Weinmannia parviflora* occurs on most of the large islands of the Societies except Raiatea and its leaf shape and indumentum vary with its ecology. *Weinmannia vescoi* and *W. raiateensis* are both confined to Raiatea. In the Marquesas, *W. marquesana* is represented by two varieties and a distinctive, new species, *W. tremuloides*, is described and illustrated from Fatu Hiva.

MOTS CLÉS
Weinmannia,
Cunoniaceae,
Iles de la Société,
Iles Marquises,
Rapa.

RÉSUMÉ
Six espèces, appartenant à la sect. *Leiospermum*, sont reconnues pour la région. *Weinmannia rapensis* est confiné à l'île de Rapa dans les Australes et sa présence à Pitcairn est discutée. *Weinmannia parviflora* se rencontre dans la plupart des grandes îles de la Société, sauf à Raiatea, avec une grande variabilité dans la forme des feuilles et la pubescence. *Weinmannia vescoi* et *W. raiateensis* sont tous deux propres à Raiatea. Pour les Marquises, *W. marquesana* compte deux variétés et une espèce nouvelle, *W. tremuloides*, endémique de Fatu Hiva, décrite ici et illustrée.

In SE Polynesia, to the east of the Cook Islands, *Weinmannia* is found in the Society Islands, the Marquesas Islands, and on Rapa in the Austral Islands. The genus is a significant component of the vegetation on Tahiti and on several of the Marquesas, in contrast to much of the Malesian-Pacific region where it is generally locally common at most.

With the exception of *Weinmannia rapensis* which is morphologically distinct and geographically isolated, material from this region of the Pacific is rather variable, especially in the shape, size and texture of the leaves. This treatment recognises five species from the Society and Marquesas Islands, including a new one from Fatu Hiva (Table 1).

The leaves of the newly named species are very distinctive but the remaining taxa are inclined to grade into one another to some extent, and the characters that differentiate between them often overlap or are not completely diagnostic. Provenance must therefore be used occasionally in identification. While this is not generally a recommended taxonomic practice, the underlying morphological and geographical patterns would otherwise be lost.

For example, *Weinmannia parviflora* appears to be confined to the Society Islands but a few specimens from the Marquesas (belonging *W. marquesana* var. *marquesana*) are vegetatively difficult to distinguish from it. Most collections of *W. raiateensis* have small, delicate leaves but a few have larger ones and/or some unifoliolate leaves, and thus resemble some specimens of *W. parviflora* from Tahiti. Material from Huahine, designated here as *W. parviflora*, is somewhat intermediate between that species and *W. raiateensis* (in having caducous stipules and winged petioles when the leaves are trifoliolate).

A large number of recent collections, especially by J. FLORENCE, provide a detailed picture of variation in relation to ecology and distribution. *Weinmannia parviflora* and *W. marquesana* especially show phenotypic variation correlated with altitude and exposure. At mid elevation on Tahiti, *W. parviflora* has narrowly elliptical leaves with a crenate-sinuate margin, while at higher altitude the leaves are shorter and often ovate, the stems

TABLE 1.—The species of *Weinmannia* in the SE Polynesia according to recent treatments.

Current revision	Bernardi (1964)	Fosberg & Sachet (1972)	Florence (1982)
Society Islands			
W. parviflora	*W. parviflora*	*W. parviflora* var. *parviflora* (by implication)	*W. parviflora* var. *parviflora*
W. vescoi (syn. *W. ovalifolia*)	*W. vescoi* (syn. *W. ovalifolia*)		*W. vescoi*
W. raiateensis	in synonomy under *W. vitiensis*		*W. raiateensis*
Marquesas Islands			
W. marquesana var. *marquesana*	*W. marquesana*	*W. parviflora* var. *marquesana* + *W. parviflora* var. *glabrata*	
W. marquesana var. *myrsinites*		*W. parviflora* var. *myrsinites*	
W. tremuloides			
Austral Islands			
W. rapensis	*W. rapensis*		*W. rapensis*

are thicker and often more densely pubescent, the internodes are shorter and the leaf margin is almost entire. A similar pattern is seen, though rarely, in *W. marquesana*. It appears that these high altitude forms have evolved in parallel on Tahiti and in the Marquesas. *Weinmannia parviflora* is absent from Raiatea and material with rounded leaves and short, glabrous internodes (*W. vescoi*) is not obviously derived from any other taxon. Thus on Raiatea, Tahiti and some of the Marquesas, there are specimens from relatively exposed, windswept sites at high altitude with ovate or rounded, coriaceous leaves and short internodes, but they all belong to different taxa depending on the island on which they occur.

Weinmannia has small, comose, anaemochorous seeds that appear to be well adapted to wind dispersal. It is thus not surprising that representatives of the genus are found on all the high volcanic islands of this region. The seeds of *W. marquesana*, *W. raiateensis* and *W. vescoi* are similar to one another and unusual in sect. *Leiospermum* in that the comose hairs are relatively short, and shorter than those of *W. parviflora* from Tahiti. If the presence of these hairs is related to dispersal, this could indicate a decline in the dispersability of these three taxa. The Iles sous le Vent (including Raiatea, Tahaa, Huahine, Bora Bora) and the Marquesas are older than the Iles du Vent (Tahiti and Moorea), Tahiti being about one million years old (see BROUSSE 1993).

A generic description applicable to the Pacific species of *Weinmannia*, and general notes on morphology, are given in HOPKINS (1998a). All the species of the region dealt with here belong to sect. *Leiospermum*, whose characters are also discussed in HOPKINS (1998a). An index to all the taxa of Malesian-Pacific *Weinmannia* (see HOPKINS 1998a,b,c) is given at the end of this paper.

Key to the species and varieties of Weinmannia in the C Pacific

1. Leaves usually trifoliolate 2
1'. Leaves usually simple (unifoliolate) 4
2. Young stems ± glabrous, petiole usually glabrous; stipules not recurved and usually caducous 3
2'. Young stems densely pubescent, petiole semiterete but not winged, pubescent; stipules strongly recurved and usually persistent (Rapa) .... **6. W. rapensis**
3. Petiole laterally flattened and U-shaped in cross section (Fatu Hiva) .... **5. W. tremuloides**
3'. Petiole ± flat on adaxial surface, not laterally flattened (Raiatea) .... **2. W. raiateensis** (and rarely some specimens of *W. parviflora* but not on Raiatea)
4. Young stems completely glabrous (Raiatea) .... **3. W. vescoi**
4'. Young stems with sparse to dense indumentum 5
5. Stipules usually persistent and elliptical, recurved, the apex rounded; capsules small, 2.5-3.5 mm long at dehiscence (Society Islands) .... **1. W. parviflora**
5'. Stipules usually caducous, when present usually ± round, conduplicate, the apex acute and the margin sometimes toothed, or sometimes stipules elliptical-ligulate; capsules larger, 3.3-5 mm at dehiscence (Marquesas) 6
6. Leaves elliptical or ovate, large (2.5-)3.3-7.5 × (1-)1.3-3.6(-4.4) cm, venation usually visible on adaxial surface and reticulum on abaxial surface not dense .... **4a. W. marquesana** var. **marquesana**
6'. Leaves ovate, smaller, 1.6-2.7(-3.3) × 0.7-1.7 cm, venation obscure on adaxial surface and reticulum on abaxial surface dense .... **4b. W. marquesana** var. **myrsinites**

1. Weinmannia parviflora G. Forst.

Fl. Ins. Austr.: 29 (1786); Willd., Sp. Pl., ed. 4, 2: 438 (1799); Poir., Encycl. 7: 580 (1806); A. Gray, U.S. Expl. Exped., Phan. 1: 673, Atlas t. 85A, Fig. 1-5 (1856) p.p.; Decne., Voy. Vénus, Bot. Texte: 26, Atlas t. 20 (1846); Seem., Fl. Vit.: 109 (1865); Engl., Linnaea 36: 647 (1870) pro parte, Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Bernardi, Bot. Jahrb. Syst. 83: 195, t. 39 (1964); Fosberg & Sachet, Micronesica 8: 44 (1972).—*Leiospermum parviflorum* (G. Forst.) D. Don, Edinburgh New Philos. J. 9: 91 (1830) pro parte excl. spec. New Zealand.—*Merretia terminalis* Banks & Sol., mss. *Marattia terminalis* Sol. in Parkinson, Drawings of Tahit. Pl., t. 48, ex Seem., Fl. Vit.: 109 (1865), pro syn. sub *Weinmannia parviflora*; Britten, J. Bot. 45: 315 (1907).—*Weinmannia parvi-*

flora var. *parviflora*; implied by Fosberg & Sachet, Micronesica 8: 44 (1972).—Type: *Forster s.n.*, s.loc., Pallas Hb. (lecto- here designated, BM! pro parte excl. left hand part of sheet).

Shrub or tree 1-10(-12) m high and up to 45 cm dbh. Branching usually not dichotomous at lower elevation, more often dichotomous at high elevation. Young stems usually densely covered in erect, stiff hairs ca. 0.4 mm long, sometimes glabrate; at lower altitudes, internodes up to 5 cm long; at high altitude internodes usually short, 0.5-1.5 mm long, the stems often thick, up to 0.3 mm diameter and nodes thickened, older stems glabrescent, ca. 0.5 mm diameter with numerous pale lenticels. Stipules usually persistent at several nodes on reproductive shoots (except Moorea and Huahine), elliptical, spathulate or ± orbicular, the margins recurved and the whole stipule recurved, 0.4-0.5(-0.9) × 0.5-0.6 (-0.8) cm, the apex rounded, puberulent on both surfaces, venation usually indented above. Leaves usually unifoliolate, sometimes mixed with trifoliolate ones. Unifoliolate leaves somewhat variable in shape and texture according to altitude: at mid altitude, subsessile to petiolate, the petiole ± terete to semiterete, 0.2-1 cm long, the blade usually narrowly elliptical, 3.5-8.8 × 1.2-3(-3.5) cm, the base either acute and decurrent into the petiole or more truncate with a sharp distinction between petiole and blade, apex acute, the blade chartaceous, sometimes punctate below, the margin sometimes thickened, crenate, dentate or sinuate and sometimes undulate, 10-15 notches on each side of a leaf; at higher altitude, shortly petiolate, the petiole ca. 0.3 mm or 0.5 mm if blade cuneate at base, the blade 3.1-5.7(-7) × (1.5-)1.9 × 3.3(-4.2) cm, ovate to oblong, the base usually truncate, the apex broadly acute to obtuse (rarely rounded), coriaceous or subcoriaceous, margin crenulate. Trifoliolate leaves up to 9 cm in length, the petiole 1-1.5 cm long; on Tahiti the petiole terete to semiterete, the upper surface not winged; on Moorea and Huahine, the petiole narrowly winged; lateral leaflets acute and unequal at base; terminal leaflet long-attenuate at base.

Inflorescence a pentad (especially at high elevation) or heptad, often with additional racemes arising at the lower most node of the inflorescence from lateral auxiliary buds; reduced leaves sometimes present at nodes within inflorescence; peduncles and rachis segments 0.5-4 cm long, shorter at higher altitude, puberulent; racemes up to 13.5 cm long at lower altitude and to 6 (-9.5) cm long at high altitude. Stipules at nodes within inflorescence smaller than at vegetative nodes. Floral buds inserted singly; floral bracts to 0.4-0.7 mm long, subcarinate, strigose-puberulent, usually caducous. Flowers usually unisexual, rarely bisexual or ?protandrous: pedicel 0.8-2.5 mm long, puberulent; calyx lobes 0.4-0.9 mm long, puberulent on outer surface; corolla oblong to ± bluntly triangular, 0.7-1.6 × 0.5-1.5 mm; disc lobes 0.3-0.7 mm long; in male flowers: filaments 1.9-3 mm long, the ovary 0.5-0.9 mm long, puberulent and the style 0.1-0.2 mm long, curved inwards; in female flowers: filaments 0.7-1.1 mm long, the ovary > 1.1 mm long at anthesis, puberulent, and the styles > 0.7 mm long, ± straight, the stigmas capitate and papillose.

Capsules 2.5-3.5 × 1.5 mm at dehiscence (up to 0.5 mm longer prior to dehiscence), the styles 0.5-0.8(-1) mm long; the exocarp sparsely puberulent to almost glabrous, endocarp sometimes separating from exocarp in old fruits; calyx lobes usually caducous; central column present. Seeds 0.8-1 mm long, comose at each end, the hairs 0.5-0.7 mm long.—Fig. 1A-K, 2.

Juvenile foliage (high altitude).—The seedling attached to *van Balgooy 1796* has simple, chartaceous leaves, up to 6.5 × 5.5 cm, with the margin dentate, the stipules much as in the adult foliage and the stem ca. 3 mm thick, woody but only sparsely hairy.

Breeding system.—Polygamodioecious. While the flowers on most specimens are either male or female, a few collections have racemes of mostly male flowers with a few bisexual ones mixed in (e.g. *Hoogland & Florence 12920*), and others have male flowers and fruit on the same specimen (*Gagné & Montgomery 2362*).

Field characters.—At lower elevations, frequently a small tree and at high elevation, a shrub or gnarled tree, the branches sometimes clothed in bryophytes. Wood red, hard (*Florence & Varney 11093*) or blaze pink and wood creamy

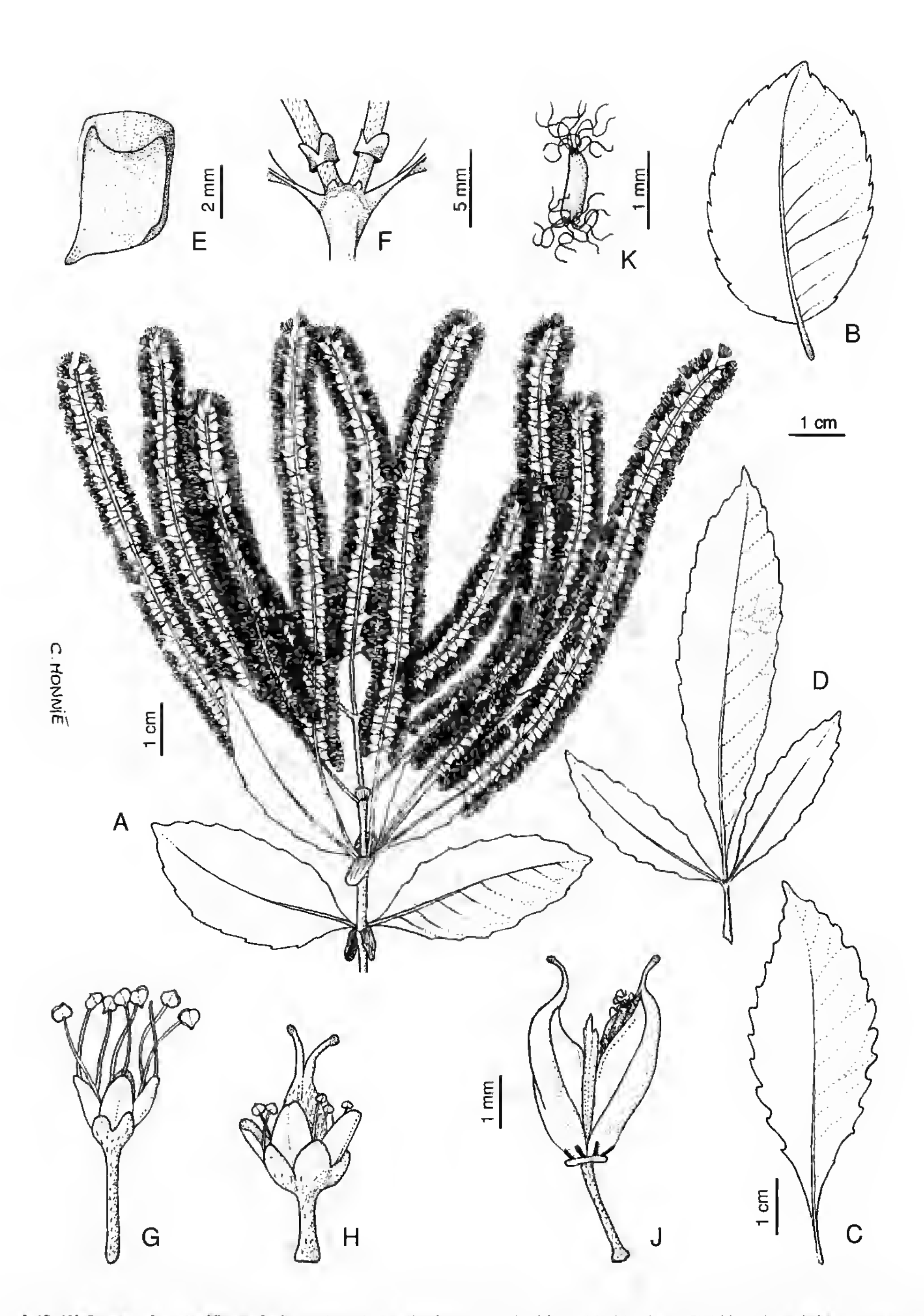


Fig. 1.—**A-K**, ***Weinmannia parviflora***: **A**, flowering shoot, the leaves typical for mid altitude on Tahiti and the inflorescence a heptad with additional racemes at the lowest node, developing from lateral auxiliary buds; **B**, leaf, typical of plants from exposed locations at high altitude on Tahiti; **C**, leaf, from Moorea; **D**, trifoliolate leaf, Tahiti; **E**, stipule with recurved margins; **F**, detail of node with 2 opposite petioles and the peduncles of 2 partial inflorescences, the apical bud aborted; each peduncle with a "collar" (remnants of fused stipules that protect the inflorescence in bud) and lateral auxiliary buds at base; **G**, male flower; **H**, female flower; **J**, dehisced capsule with persistent central column and one seed remaining in locule; **K**, seed. (A, E, G, *Florence 9090*; B, *St. John & Fosberg 17146*; C, *Florence 8365*; D, H-K, *Florence 9089*; F, *Florence 3110*).—Drawn by C. MONNIÉ.

(*van Balgooy 1685*). Leaves pale green or bright green above, shiny, coriaceous. Inflorescence axes and calyx show a colour polymorphism at lower altitudes, being either pale green or purple-red, but above 1500 m only the red form was observed (J.C. BRADFORD pers. comm.). Buds white or red. Flowers with pedicel and sepals pinkish, pale purple or green, petals and stamens white, disc segments pale purple or dark, anthers yellow, ovary white or pale green, the stigmas pinkish in female flowers (specimen field labels and J.C. BRADFORD pers. comm.). Reported as odourless (*Quayle 39*) or sweetly scented and visited by bees (J.C. BRADFORD pers. comm.). Fruit green sometimes tinged with red, reddish, or pale purple; later brown.

DISTRIBUTION AND ECOLOGY.—Abundant on Tahiti and also occurring on Moorea, Huahine and Bora Bora [*fide* FLORENCE (1982), who reports that *Dumont d'Urville 200* (s.l., s.d.) is from that island]. Also grows on Tahaa (J. FLORENCE pers. obs.).

On Huahine, confined to the central crest between Mt. Matoereere and Mt. Turi, from 450 m to the summit (670 m), in forest dominated by *Metrosideros* and *Macaranga*, growing with *Alstonia* and *Myrsine*, and especially recorded from ridges. On Moorea, first appearing around 400-500 m, and co-dominant with *Metrosideros* in mesic forest and more abundant in cloud forest with *Ilex*, *Myrsine* and *Metrosideros* up to 1200 m. On Tahiti, probably the most abundant woody plant in undisturbed forest from 400 m to the summit of the island, Mt. Orohena, at 2241 m. Co-dominant with *Metrosideros* as the main structural element of slope and ridge forest at medium and high elevations and practically ubiquitous. Other associates in moss-covered shrubbery at high altitude in the typical *Weinmannia-Alstonia* forest (FLORENCE 1993) include *Myrsine*, *Coprosma*, *Cyathea*, *Alstonia*, *Vaccinium*, *Alyxia*, *Reynoldsia*, and *Ilex*. At lower elevations, it occurs with *Alphitonia*, *Dodonea* and *Psidium* and is also found in scrub, on *Dicranopteris*-covered slopes and on steep wooded escarpments.

SELECTED COLLECTIONS (from a total of 88 studied).—**SOCIETY ISLANDS**: ***Bora Bora***?: *Dumont d'Urville 200*, s.loc., fr. (P). ***Huahine***: *Florence & Tahuaitu 11627*, crête entre les Mts. Mato Ereere et Moua Turi, 16°43'S-151°01'W, 610 m, fl., 30 Oct. 1992 (P, PAP); *Grant 5314*, Distr. Maeva, Matoereere, 1710 ft., fl., 7 Feb. 1931 (BISH); *Grant 5316*, seedling (BISH); *St. John 17159*, Huahine Nui, Mt. Matoereere, N ridge, 650 m, fr., 1 Oct. 1934 (A, BISH, K, P). ***Moorea***: *Florence 7935*, Haumi, crête SE du Mt. Tohiea, 17°33'S-149°49'W, 860 m, fl., 22 Oct. 1986 (BISH, K, P, PAP); *Florence 8365*, Mt. Tohiea, sommet N, 17°33'S-149°49'W, 1200 m, buds, 9 July 1987 (BISH, P, PAP); *Smith 174*, plateau above Afareaitu, fl., 8 June 1967 (A, BISH). ***Tahiti***: *Adamson 40*, Distr. of Hitiaa, 400 m, buds, 19 Nov. 1928 (BISH); *Carlquist 655*, between Rocher du Diable and Fare Mato on Aorai Mt., 4200 ft., fr., 15 June 1962 (GH); *Florence 2291*, sentier captage d'eau du Belvédère, 17°34'S-149°31'W, 620 m, fr., 14 Jan. 1982 (P, PAP); *Florence 2315*, sentier du Mt. Marau, au Pic Vert, 17°37'S-149°32'W, 1405 m, fl., fr., 28 Jan. 1982 (BISH, P, PAP); *Florence 3277*, Mt. Marau, env. du relais TV, 17°37'S-149°32'W, 1430 m, yfr., 5 June 1982 (BISH, K, P, PAP); *Florence 3353*, route du Pic Rouge, Propriété Lévy, 17°35'S-149°33'W, 630 m, fr., 17 June 1982 (BISH, K, P, PAP); *Florence 3645*, crête W de la Papenoo, sentier de l'Orohena, 17°33'S-149°26'W, 915 m, fr., 3 Aug. 1982 (BISH, K, P, PAP); *Florence 5462*, Mahina, sommet du Mt. Pitohiti, sentier de l'Orohena, 17°37'S-149°28'W, 2110 m, fr., 19 Oct. 1983 (P, PAP); *Florence 7186*, Mahina, sommet N de l'Orohena, flanc S, 17°37'S-149°29'W, 2215 m, buds, 16 Nov. 1984 (P, PAP); *Florence 9088*, Faaa, route du Mt. Marau, km 6.5, 17°37'S-149°34'W, 1080 m, fl., 11 Feb. 1988 (BISH, P, PAP); *Florence & Varney 11093*, Punaauia, vallée Maruapo, crête N, 17°39'S-149°35'W, 880 m, fl., 13 Feb. 1992 (P, PAP); *Fosberg 62927*, NW slope up to Pic Vert, headwaters of side branches of R. Tipaerui, 640-650 m, fr., 17 June 1982 (BISH, BM, K, P, PAP); *Gagné & Montgomery 2362*, Mt. Orohena, 2240 m, fl., 11 Sep. 1988 (BISH); *Gagné 1013*, Mt. Marau, 1493 m, buds, fr., 30 June 1977 (BISH, P); *Grant 3601*, Dist. Punaauia, Diadem, 3275 ft., fl., 14 May 1930 (BISH); *Hoogland & Florence 12916*, Faaa, Mt. Marau, ridge towards Pic Vert, below TV station, 1380 m, fl., 14 Mar. 1994 (MO, P, PAP); *Hoogland & Florence 12918*, ridge between Upper Faatautia River and Paaraura valley, 600 m, fr., 16 Mar. 1994 (MO, P, PAP); *Hoogland & Florence 12927*, Taiarapu Peninsula, plateau de Taravao along ridge track in upper Amoa catchment, 680 m, fr., 17 Mar. 1994 (MO, P, PAP); *Hoogland & Florence 12931*, between Lac Vaihiria and Col Urufaau, 650 m, fl., 24 Mar. 1994 (MO, P, PAP); *MacDaniels 1313*, S side Orohena, 1500 m, fl., 16 May 1927 (A, BISH, K); *MacKee 3056*, plateau below summit of Mt. Aorai, 1800-2000 m, fl., 27 Aug. 1955 (K); *Moseley, Challenger Expedition s.n.*, s.loc., 4000 ft., Sep. 1875,

(BM, K); *Nadeaud 413*, crêtes du Pinai et du Tafifi, fl., Dec. 1856 (P); *Quayle 39*, Mt. Aorai Trail, leaward, 1694 m, fl., fr., 22 Sep. 1921 (BISH, K); *Raynal & Taureau 16539*, piste de l'Aorai, entre Belvédère et Fare Hamura, 600 m, buds, 6 Oct. 1971(P); *St. John & Fosberg 17146*, Orofena, S ridge, 1570 m, fr., 25 Sep. 1934 (A, BISH, P); *Teraoka & Kennedy 113*, Papenoo, back of Eric Garnier property, fr., 6 Sep. 1979 (BISH); *van Balgooy 1790*, NW ridge of Aorai, 1700 m, fl., fr., 22 Sep. 1971 (L).

LOCAL NAMES.—Aito; Aito mou'a; Ouru. Local uses: firewood (*Quayle 39*).

TYPIFICATION.—*Weinmannia parviflora* was the first species in the genus to be described from this part of the Pacific and its taxonomic history is discussed by BERNARDI (1964: 195). It was described by G. FORSTER, who with his father, was naturalist on the second of Captain COOK'S circumnavigational voyages in the H.M.S. Resolution from 1772 to 1775 (FOSBERG 1993). According to MERRILL (1954: 206), the name *W. parviflora* was one of several that were appropriated by FORSTER from the unpublished manuscript of SOLANDER and for which the latter had already prepared a detailed description based on the BANKS & SOLANDER collections from the first of COOK's voyages. However, many of the descriptions in FORSTER's Prodromus (1786) were actually written during the second voyage and D. NICOLSON (pers. comm.), who is studying the FORSTER types, considers it entirely appropriate to choose one of the specimens in the FORSTER collections as the lectotype.

The sheet selected at BM contains two elements. The right hand piece is designated as the lectotype of *Weinmannia parviflora* and the left hand piece belongs to *W. racemosa* L. f. from New Zealand. Both of COOK's expeditions went on to collect in New Zealand after visiting Tahiti. Records of *W. parviflora*, mostly under the name *Leiospermum parviflorum*, from New Zealand [e.g. by D. DON (1830), WALPERS (1846), G. DON (1834)] are due to confusion with *W. racemosa*. Both species usually have simple leaves of similar size but the inflorescence structure is different (see HOPKINS 1998a).

Several early authors [e.g. GRAY (1854), MUELLER (1858), SEEMANN (1865), DRAKE (1890)] also included material of *Weinmannia rapensis* in their concept of *W. parviflora*, based on *Cuming 1428*. These records from Elizabeth Island, (now Henderson Island in the Pitcairn group) are discussed under *W. rapensis*.

VARIATION.—*Weinmannia parviflora* is especially variable in the shape of its leaves or leaflets, but the young stems are usually pubescent and the stipules strongly recurved and usually persistent. On Tahiti, *W. parviflora* shows variation in leaf shape with altitude, and our concept of this species differs from BERNARDI's in including all the high altitude material with ovate or rounded leaves here, rather than in *W. vescoi*, which is endemic to Raiatea. At middle elevations, the internodes of *W. parviflora* are relatively long and the leaves are usually narrowly elliptical with the margins markedly crenate or sinuate (Fig. 1A), and some trifoliolate leaves occur (Fig. 1D). At high elevation, in the central massif on Mt. Aorai, Mt. Orohena and Pito Hiti, the leaves are often shorter, usually oblong or ovate and the margins less markedly crenate (Fig. 1B) and the internodes are short, so that the overall habit resembles that of *W. vescoi*. Between 1500-1600 m on the flanks of Mt. Aorai, adjacent trees can have contrasting leaf morphologies (J.C. BRADFORD pers. comm.). Most collections are densely pubescent on the young stems but a few are glabrous (e.g. *Gagné & Montgomery 2362*, *Florence 7186*; *Florence 5464* is ± glabrous).

Material from Huahine, designated here as *Weinmannia parviflora*, has some similarities with *W. raiateensis* since the stipules are caducous and the petioles are winged when the leaves are trifoliolate. Collections from Moorea also differ somewhat from *W. parviflora* in Tahiti as the stems are more or less glabrous, the stipules are rarely persistent and the leaves, although unifoliolate, have a rather sinuate and/or undulate margin (Fig. 1C).

2. Weinmannia raiateensis J.W. Moore

Bernice P. Bishop. Mus. Bull. 102: 29 (1933); Bernardi, Bot. Jahrb. Syst. 83: 207 (1964) under *W. vitiensis*.—Type: *J.W. Moore 396*, Society Islands,

Raiatea, on high ridge between Vairahi and Avera Rahi valleys, 300 m, 3 Dec. 1926 (holo-, BISH; iso-, BISH!, P! 2 sheets).

Shrub or small tree 0.4-5 m high. Branching sometimes dichotomous. Nodes scarcely thickened and annular scar not prominent; internodes 0.5-3.8 cm. Young stems sparsely strigose-pubescent or glabrous. Stipules caducous or not, elliptical, shortly spathulate to ligulate, sometimes recurved, 0.7-1.1 × 0.4-0.6 cm, apex rounded to obtuse, ± glabrous with short, adpressed hairs towards base on abaxial surface. Leaves mostly trifoliolate, sometimes some unifoliolate, total length up to 9.7 cm (for a trifoliolate leaf) including a petiole of 0.4-2.4 cm; petiole semiterete and narrowly winged especially towards point of insertion of leaflets, glabrous or rarely pubescent above or below; leaflets narrowly elliptical, elliptical or narrowly obovate, the lateral ones 2.3-6 × 0.7-1.7 cm, base cuneate and unequal, apex acute, the terminal ones 3.8-8.3 (including a petiolule of 0.4-1.5) × 1.2-1.9 cm, base long attenuate, apex usually acute, often broken; the blade glabrous on both sides, chartaceous to subcoriaceous, not punctate; margin sometimes thick-ened, crenate, 9-14 notches on each side of a leaflet, midrib flat or slightly raised above, prominent below, secondary and tertiary venation flat or slightly raised on both sides.

Inflorescence rather variable and nodes often asymmetrically branched; either a central triad or pentad, or two lateral triads, the apical bud aborted; often arising at nodes other than the most distal on a shoot; peduncle and rachis segments shortly and sometimes densely pubescent, peduncle 0.6-1.1 cm long, rachis segments up to 5 cm long. Floral buds inserted singly; floral bracts 0.6-0.7 mm long, scarcely longer than the buds, ligulate, ± glabrous, caducous. Flowers unisexual (male, *Gagné 1457*; female, *Florence 8945*); pedicel 1-1.7 mm long; calyx lobes 0.6-0.7 mm long, glabrous; petals 1.1-1.3 × 0.8 mm, oblong; in male flower: filaments ca. 2.5 mm long, disc lobes 0.4 mm long, ovary 0.7 mm long, pubescent, styles 0.1 mm long, incurled; in female

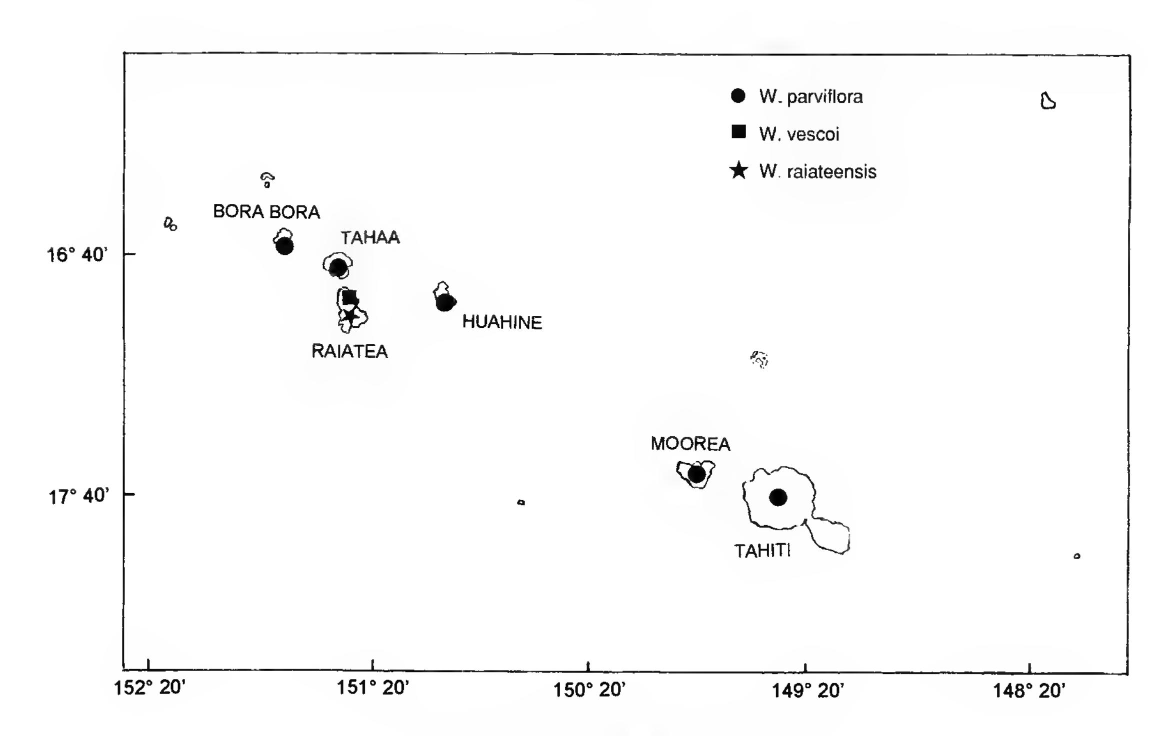


Fig. 2.—Distribution of ***Weinmannia*** in the Society Islands.

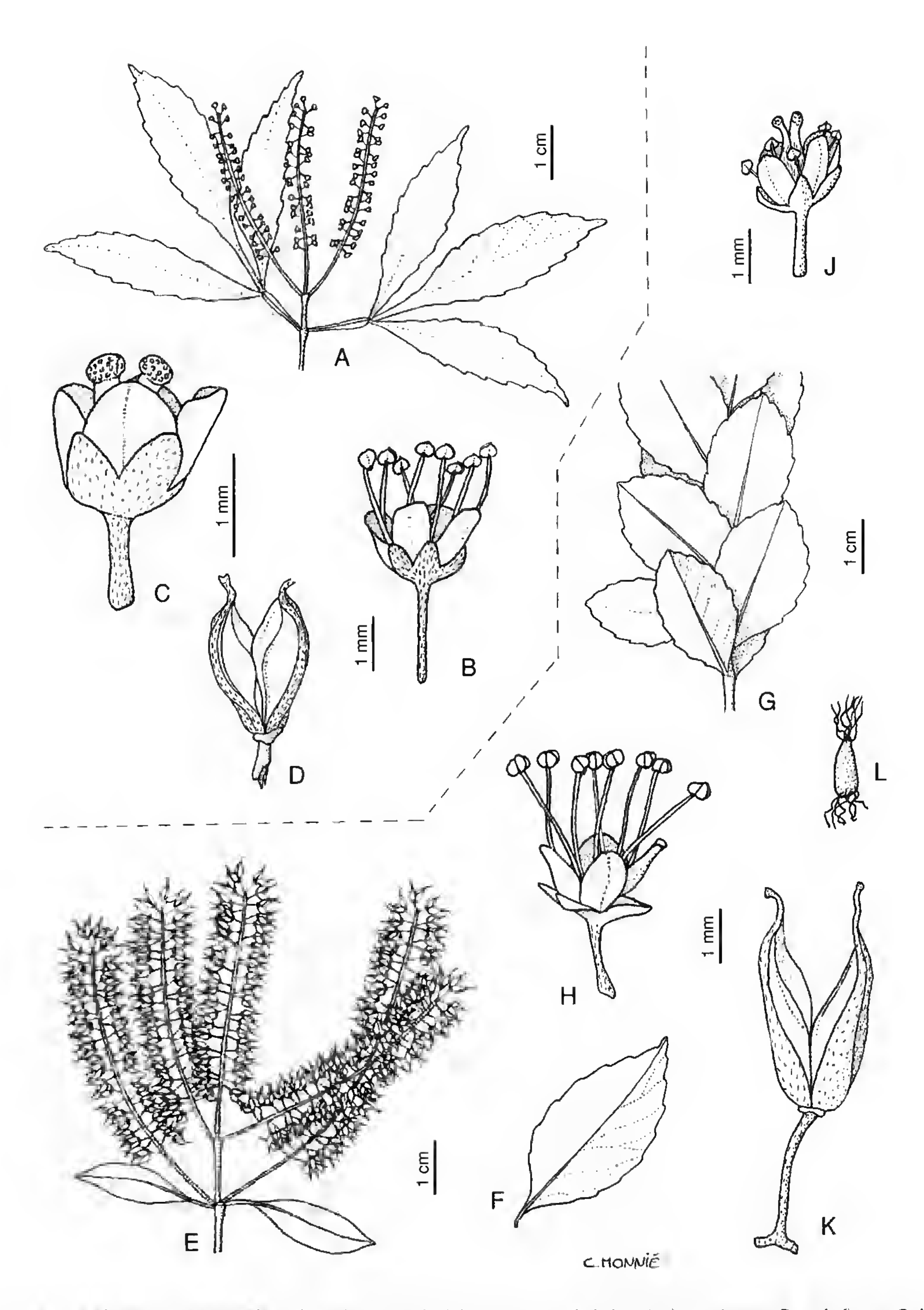


Fig. 3.—**A-D**, ***Weinmannia raiateensis***: **A**, flowering stem, the inflorescence a triad, the stipules caducous; **B**, male flower; **C**, female flower; **D**, dehisced capsule. (A, *Florence 5143*; B, *Gagné 1457b*; C, *Florence 8945*; D, *Florence 3746*).—**E-L**, ***Weinmannia vescoi***: **E**, shoot with infructescence (pentad); **F**, single leaf; **G**, section of a stem with short internodes and imbricate leaves; **H**, male flower; **J**, female flower; **K**, dehisced capsule; **L**, seed. (E, F, K, L, *Gagné 1454*; G, *Florence 3586*; H, *Florence 5197*; J, *Florence 8991*).—Drawn by C. Monnié.

flower: filaments 0.8-1 mm long, disc lobes 0.7 mm long, ovary 1-1.2 mm long, ± glabrous, styles 0.9-1 mm long, the stigmas capitate.

Capsules 1.5-3.2 × 0.9-1.8 mm at dehiscence, the styles ca. 0.5 mm long, exocarp glabrous; calyx lobes caducous, central column present. Seeds 0.6 mm long, comose at both ends, the hairs short, 0.4 mm, and not very abundant.—Fig. 2, 3A-D.

JUVENILE FOLIAGE.—*Florence 3746b* consists of regrowth shoots from the base of the trunk. The leaves are 3-5-foliolate, chartaceous, and the apical leaflet is almost rhombic and broader than in the adult foliage.

BREEDING SYSTEM.—Limited herbarium material has only unisexual flowers, but this species is in fact polygamodioecious (J.C. BRADFORD pers. comm.).

FIELD CHARACTERS.—Leaves pale green. Inflorescence rachis purplish; buds white or cream; flowers pale yellow to white. Fruits red or pale purple.

DISTRIBUTION AND ECOLOGY.—Endemic to Raiatea where it is relatively widespread but rather scarce, from 300-965 m. A species typical of hygrophilous vegetation at mid altitude with *Metrosideros*, *Glochidion* and *Myrsine*, or in cloud forest with *Ilex*, *Macaranga* and *Astronidium*. It does not occur in the same habitats as *Weinmannia vescoi* (see below).

MATERIAL EXAMINED.—**SOCIETY ISLANDS**: ***Raiatea***: *Florence 3554*, Plateau de Temehani Rahi, 16°47'S-151°27'W, 690 m, fr., 3 July 1982 (PAP); *Florence 3746*, ibid., 760 m, fr., 25 Aug. 1982 (BISH, K, P, PAP); *Florence 3746b*, ibid., regrowth, 25 Aug. 1982 (P, PAP); *Florence 3754*, ibid., flanc NW, 740 m, fl., 25 Aug. 1982 (P, PAP); *Florence 5143*, côte E, Avera, Crête S de la Paipai, 16°48'S-151°26'W, 395 m, 13 Sep. 1983 (P, PAP); *Florence 8945*, Tevaitoa, crête sommitale du Mt. Toomaru, 16°50'S-151°27'W, 965 m, fl., 27 Nov. 1987 (P, PAP); *Gagné 1457b*, Mt. Temehani, NE side, 740 m, 3 Sep. 1977 (BISH, P).

BERNARDI (1964) placed *Weinmannia raiateensis* in synonomy under *W. vitiensis* Seem. on the basis of the type description. Both have trifoliolate leaves but in *W. raiateensis* they are generally smaller and more delicate, although there is some overlap. Several other species in sect. *Leiospermum* in the Pacific have trifoliolate or imparipinnate leaves with a somewhat winged petiole, including *W. croftii*, *W. sp.* (Solomons A) and *W. denhamii* (HOPKINS 1998c). Although distinctions between taxa are slight, there are differences in mean leaflet shape and dimensions. This particular leaf morphology has thus either evolved several times or else these species originate from a single trifoliolate/imparipinnate ancestor that has been dispersed amongst a number of volcanic islands and differentiated only slightly on each.

3. Weinmannia vescoi Drake

Ill. Fl. Ins. Pacif.: 35, t. 13 (1886); Fl. Polynésie Franç.: 61 (1893); Bernardi, Bot. Jahrb. Syst. 83: 206 (1964).—Type: *Vescoi s.n.*, Tahiti (*sic*, but probably from Raiatea) (holo-, P!).

Weinmannia ovalifolia J.W. Moore, Bish. Mus. Bull. 102: 28 (1933).—Type: *Moore 95*, Society Islands, Raiatea, S facing slope along path to Mt. Temehani, 18 Sep. 1926 (holo-, BISH; iso-, BISH!, L!).

Low shrub to small, multi-stemmed tree 0.15-4 m high × 5+ cm diameter. Stems often sparsely branched or unbranched for long sections; branching rarely dichotomous. Nodes thickened and "kneed", the internodes laterally contracted, 0.5-2.5(-7.5) long × ca. 1 mm thick. Stems glabrous, smooth with fine longitudinal striations, lenticels few, on lower parts of stems. Whole plant largely glabrous except for sparse puberulence sometimes present on stipules, inflorescence axes, pedicels; leaves, calyx and exocarp often warty. Stipules usually caducous, elliptical, ligulate or rarely orbicular, 0.3-0.7 × 0.2-0.4 cm, apex acute or rarely rounded, ± flat or rarely recurved, ± glabrous to puberulent. Leaves unifoliolate, (rarely trifoliolate and then the petiole winged), the petiole 0.2-0.6 cm long, the blade elliptical, broadly elliptical or ovate, 1.8-4.7(-6.4) × 1-2.5(-5.5) cm, base truncate to acute and shortly decurrent, apex acute, obtuse or rounded, subcoriaceous to coriaceous, rarely punctate below, margin sometimes thickened, crenate, crenations more pronounced in smaller ovate or elliptical leaves, 9-12 notches on each side of each leaf, midrib raised and ridged above, prominent

below, secondary venation obscure, flat or slightly indented above, slightly raised below.

Inflorescence usually a pentad sometimes with two lateral triads, rarely a heptad, reduced leaves sometimes present at nodes within inflorescence; peduncles and rachis segments glabrous or sparsely puberulent, 0.5-1.2(-2.5) cm long, racemes 2.5-5 cm long. Floral buds inserted singly; floral bracts 0.7-1.4 mm long, ± equal in length to buds or longer, ligulate to subcymbiform, minutely ciliate on margin, caducous. Flowers mostly unisexual, rarely bisexual; pedicel 1.4-2.1 mm; calyx lobes 0.6-1 mm long; corolla 1-1.7 × 0.6-1.2 mm, oblong; disc lobes 0.3-0.6 mm; in male flowers: filaments 2.7-3.4 mm long, anthers 0.3-0.4 mm diameter, ovary 0.6-1.1 mm, styles 0.1-0.3 mm; in female flowers: filaments 0.7-1.2 mm long, ovary 1-1.5 mm, styles 0.7-1 mm, stigmas capitate, papillose; in bisexual flowers: filaments 1.5-3.3 mm, ovary 1.2 mm, styles 0.7 mm.

Capsules 2.1-4.0 × 1.5-1.8 at dehiscence, styles 0.5-1 mm long, stigmas capitate, exocarp glabrous with longitudinal striations, endocarp sometimes separating from exocarp; calyx lobes caducous, central column present. Seeds ca. 0.8 mm long, comose at both ends, the hairs 0.3 mm long.—Fig. 2, 3E-L.

BREEDING SYSTEM.—Polygamodioecious. Most specimens have male or female flowers (e.g. *Moore 793*, *St. John 172555*, *Florence 5197*, male; *Florence 5203*, *8991* and *Hoogland 12929*, female), *Gagné 1454* has some apparently bisexual flowers, and *Grant 5197* has mature capsules and male flowers on the same shoot.

FIELD CHARACTERS.—Growth form rarely with a central trunk, but usually with numerous tall stems arising from the base; often distinctive with long, sparsely branched, stiff twigs with short internodes and thickened nodes, the twigs often well covered with unifoliolate, opposite and decussate, elliptical to rounded leaves. *Morat 6996* shows an extreme growth form from dense scrub in an exposed, wind swept region of the plateau; it is a much branched chamaephyte, 15-20 cm high with small, rounded leaves. In such individuals the slender stems arise from a large woody root-mass, often visible at ground level (J.C. BRADFORD pers. comm.). Inflorescences often short, congested, not projecting beyond the leaves. Rachis of inflorescence and calyx either green or purple-red; flowers similar to those of *W. parviflora* in colour and scent (J.C. BRADFORD pers. comm.).

DISTRIBUTION AND ECOLOGY.—Endemic to Raiatea where it is locally abundant from 355-740 m. One of the species confined to the plateaux of Temehani Rahi and Temehani Ute Ute where another endemic and symbol of the island, *Apetahia raiateensis* (Campanulaceae), also occurs. Locally co-dominant with *Metrosideros*, *Astronidium* and *Alstonia*, the herb layer dominated by Cyperaceae such as *Gahnia schoenoides* or *Machaerina bidwillii*.

SELECTED COLLECTIONS (from a total of 26 studied).—**SOCIETY ISLANDS**: ***Raiatea***: *Florence 3586*, Plateau de Temehani Rahi, fin de la route, 16°46'S-151°27'W, 490 m, fr., 5 July 1982 (BISH, P, PAP); *Florence 5197*, Plateau de Temehani Rahi, secteur NE, 16°46'S-151°26'W, 510 m, fl., 16 Sep. 1983 (BISH, P, PAP); *Florence 8991*, Tevaitoa, sentier du Plateau Temehani Ute Ute, 16°47'S-151°28'W, 435 m, fl., fr., 29 Nov. 1987 (BISH, P, PAP); *Florence 10454*, Tevaitoa, Plateau de Temehani Rahi, 16°46'S-151°27'W, 530 m, fr., 10 June 1990 (BISH, PAP); *Gagné 1457* (P), *1457a* (BISH), Mt. Temehani, NE side, 740 m, buds, 3 Sep. 1977 (P, BISH); *Grant 5234*, Distr. Avera, Temehani, 1690 ft., fl., 29 Jan. 1931 (BISH); *Hoogland & Florence 12929*, N slopes of Plateau de Temehani rahi, 410 m, fr., 21 Mar. 1994 (MO, P, PAP); *Moore 793*, path to Mt. Temehani, S facing slope, fl., 1 Jan. 1927 (BISH); *Morat 6993*, montée au Temehani ute, 550 m, buds, 26 Aug. 1982 (BISH, K, P, PAP); *St. John 17255*, Temihani Plateau, 500 m, fl., fr., 5 Oct. 1934 (BISH, P); *Whistler 4906*, ibid., 650 m, fl., 3 Sep. 1981 (BISH).

The type, *Vescoi s.n.*, is labelled "Tahiti". The lower parts of the stems are glabrous although the most distal internodes are moderately hirsute and the stipules are ligulate. The inflorescence is not congested. The majority of collections from high altitude on Tahiti that have similar broadly ovate leaves (*Weinmannia parviflora*) have thicker, more densely pubescent stems, strongly recurved stipules and congested inflorescences. However, a few have glabrous stems and ligulate stipules and/or inflorescences which project beyond the foliage. The identity and provenance of *Vescoi s.n.* is thus problematical. It could either be regarded as an aberrant form of *W. parviflora*

from high altitude on Tahiti or treated, as here, as a mislabelled collection from Raiatea.

Weinmannia vescoi resembles *W. parviflora* from high altitude on Tahiti in several respects, especially in the broadly ovate, often coriaceous leaves, the short internodes and thickened nodes. However, it differs in having glabrous stems and stipules that are usually caducous, ± flat and ligulate.

Although following the same synonomy as BERNARDI, our circumscription of this species differs considerably from his, and *St. John 17255* from Raiatea is the only one of the specimens cited by BERNARDI that is referred here to *Weinmannia vescoi*; all the others cited by him are from Tahiti and placed by us in *W. parviflora*.

4. Weinmannia marquesana F. Br.

Bernice P. Bishop. Mus. Bull. 130: 99 (1935); Bernardi, Bot. Jahrb. Syst. 83: 193 (1964).

a) Weinmannia marquesana var. marquesana

Weinmannia parviflora G. Forst. var. *marquesana* (F. Br.) Fosberg in Fosberg & Sacher, Micronesica 8: 44 (1972).—*Weinmannia marquesana* var. *typica* F. Br., Bernice P. Bishop. Mus. Bull. 130: 99 (1935), nom. inval.—Type: *Brown 497*, Marquesas Islands, Nuku Hiva, To(o)vii, 1000 m, 15 July 1921 (holo-, BISH; iso-, BISH!).

Weinmannia marquesana F. Br. var. *glabrata* F. Br., Bernice P. Bishop. Mus. Bull. 130: 99 (1935).—*Weinmannia parviflora* G. Forst. var. *glabrata* (F. Br.) Fosberg in Fosberg & Sachet, Micronesica 8: 45 (1972).—Type: *Brown 1084B*, Marquesas Islands, Hiva Oa, Mount Oorua, 800 m, 15 Dec. 1921 (holo-, BISH; iso-, BISH!).

Shrub to small tree, rarely a subshrub, (0.7-) 1.5-10 m tall, up to 35 cm dbh. Young stems terete and narrow, 1-2 mm diameter, the nodes slightly thickened, ± glabrous to densely tomentose (the hairs up to 0.5 mm long) or pilose (hairs up to 0.9 mm long), older stems glabrescent, finely longitudinally fissured sometimes with pale lenticels. Branching often dichotomous. Stipules usually early caducous, either elliptical-ligulate, 0.6 × 0.2 mm the apex rounded and recurved, or diamond-shaped to broadly ovate and conduplicate 1.3-1.7 × 0.8-1.2 mm, the apex acute and the margin entire to serrulate, glabrous except for short strigose hairs on abaxial surface towards the base. Leaves simple (rarely trifoliolate), petiole semiterete, 0.3-1.8 cm long, glabrous to tomentose along mid line on adaxial surface and glabrous or more often pubescent on abaxial surface, blade elliptical or sometimes ovate, (2.5-)3.3-7.5(-9.6) × (1-)1.3-3.6(-4.4) cm, base cuneate or acutely constricted into the petiole, apex acute or sometimes acuminate, blade subcoriaceous, glabrous, sometimes punctate below, margin usually minutely thickened and revolute, minutely crenulate, crenate, serrate or rarely ± sinuate, 11-22 notches down each side; main vein flat or raised above, and sometimes minutely hairy towards the base, prominent and often shortly hairy below, secondary and tertiary venation flat on both sides, the secondary veins equidistant from one another and all arcuate towards the margin and apex at the same angle, reticulum of tertiary veins open to dense.

Inflorescence a triad or pentad (variants include 3 triads or a central triad and 2 pairs of racemes (each developing from a lateral auxiliary bud) arising from the same node as the subtending leaves), reduced leaves at nodes within inflorescence not seen, peduncles and rachis segments 0.8-2.5(-6.5) cm long, almost glabrous or sparsely to densely hairy, racemes up to 7-8(-12) cm long. Floral buds inserted singly; floral bracts to 1.6 mm long, narrowly ligulate to subcarinate, strigose-puberulent, caducous. Flowers unisexual or bisexual; pedicel 1-3.0 mm long, puberulent or not; calyx lobes 0.7-1.2 × 0.6-1 mm long, shortly strigose or glabrous on outer surface; petals oblong, 1.5-1.9 × 0.8-1.2 mm, apex rounded; disc lobes 0.4-0.8 mm long; in male flowers: filaments 2.7-3 mm long, the ovary 0.8-0.9 mm long, usually pubescent, the styles ca. 0.2 mm long, curved inwards; in female flowers: filaments 0.4-0.5 mm long, the ovary 1.1-1.5 mm long at anthesis, glabrous, and the styles 1 mm long, ± erect, the stigmas capitate and papillose, ovules up to 4 × 7 per capsule; in bisexual flowers: filaments 2.8-3.5 mm long, ovary 1.5-2.2 mm long, glabrous or with sparse short strigose hairs, styles 1.2-1.4 mm long, stigmas capitate, papillose. Infructescence often dense.

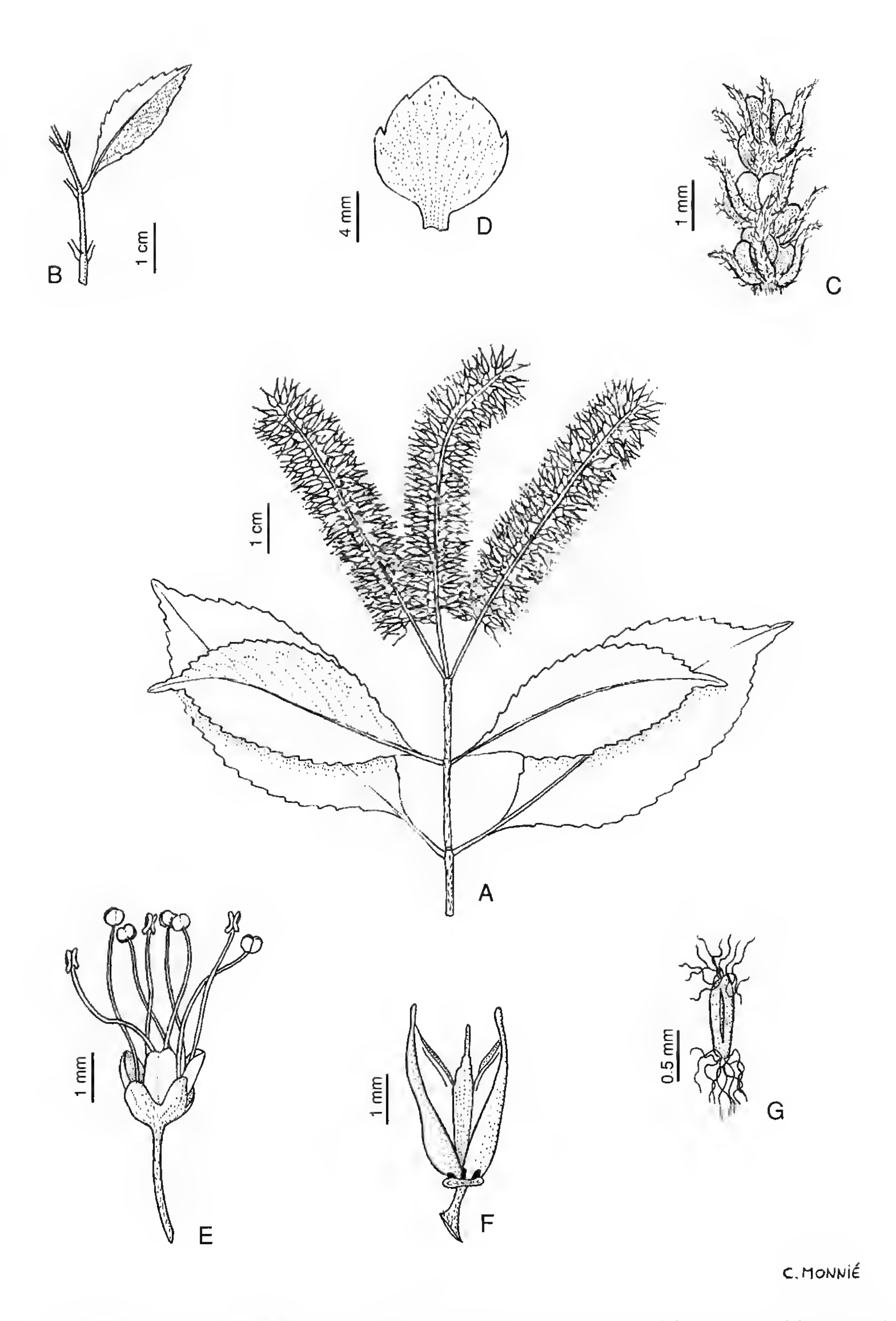


Fig. 4.—**A-G**, ***Weinmannia marquesana***: **A**, *W. marquesana* var. *marquesana*: shoot with infructescence of 3 racemes (triad), stipules caducous; **B**, *W. marquesana* var. *myrsinites*: leaf with dense reticulate venation; **C**, section of a raceme showing floral bracts and buds; **D**, stipule from a sterile shoot; **E**, male flower; **F**, fruit with persistent central column; **G**, seed. (A, *Gagné 1033*; B, *MacKee 44689*; C, *Mercier s.n. 1847*; D, *Mumford & Adamson 494*; E, *Florence 7447*; F, G, *Florence 6882*).—Drawn by C. MONNIÉ.

Capsules 3.3-5 × 1.5-2 mm at dehiscence, styles 0.5-1 mm long, exocarp glabrous or almost so, endocarp sometimes separating from exocarp in old fruits; calyx lobes caducous, central column present. Seeds 0.6-0.8 mm long, comose at each end, the hairs few and weakly developed, < 0.5 mm long.—Fig. 4A,C-G, 5.

JUVENILE FOLIAGE.—Foliage from young plants and coppice shoots is either simple (*Mumford & Adamson 139* and *Brown 1078*) or trifoliolate (*Mumford & Adamson 494*) with the stipules often persistent. As in other species, the leaflets are chartaceous or subcoriaceous. *Perlman 10204* from low forest on Hiva Oa is exceptional as it is almost glabrous, has trifoliolate leaves up to 23 cm long (terminal leaflets up to 17 × 8.5 cm) and the stipules are orbicular-reniform, 3.5 cm diameter, with the apex broadly rounded and the margin entire or dentate. This specimen is probably from a coppice shoot in shade.

BREEDING SYSTEM.—Polygamodioecious. Several sheets have male flowers and mature fruits and only 3 out of about 70 have female flowers (*Mumford & Adamson 497*, *Quayle 1253* and *Florence 7262*). There is no evidence of protandry. *Florence 7447* (P) has bisexual flowers and dehisced fruits and another sheet (BISH) has both male and bisexual flowers. This species appears to have cycles of male and bisexual flowers, with occasional plants producing female flowers.

FIELD CHARACTERS.—Variable in growth habit; when a small tree, the crown sometimes umbrella-shaped. Bark grey, brown or reddish, smooth; sapwood white or pinkish; heartwood red, fragrant. Flowers greenish-white to cream, calyx greenish-red, corolla and stamens white. Young fruits green to bright carmine red.

DISTRIBUTION AND ECOLOGY.—Marquesas Islands: Fatu Hiva, Hiva Oa, Nuku Hiva, Tahuata, Ua Huka, and Ua Pou, from 500-600 m upwards, except on Nuku Hiva where found from 790-1180 m.

This appears to be a sister species of *Weinmannia parviflora* from the Society Islands occupying the same range of habitats, from dense primary rain forest and disturbed forest at mid-elevations to cloud forest and scrub on ridges and slopes, often in exposed localities, at high altitude. It also occurs in xerophilous scrub or open areas on hilltops with *Dicranopteris*, where it resprouts after burning. It is one of the major woody plants from 790 m upwards on Nuku Hiva, locally co-dominant and increasingly common with altitude. In dry forest, scrub and savanna its main associates are *Metrosideros* and *Dicranopteris*, and also *Paesia*. In mesic forest it occurs with *Cyathea*, *Freycinetia*, *Cheirodendron*, *Santalum*, *Scaevola*, *Myrsine*, *Ilex*, *Glochidion*, *Cyrtandra*, *Trimenia*, *Hernandia*, *Metrosideros*, *Mangifera*, *Pandanus*, *Hibiscus*, *Wikstroemia*, with numerous ferns and epiphytes.

SELECTED COLLECTIONS (from a total of 67 studied).—MARQUESAS: ***Fatu Hiva***: *Brown 1078*, Omoa, 800 m, st., 4 Apr. 1905 (BISH); *Decker 2388*, along trail between Omoa and Ui'a, within 1 km of pass over central ridge, 750 m, fr., 12 Oct. 1974 (BISH, P); *Florence et al. 9490*, haut bassin de l'Uiha, E du Mt. Teamotua, 10°28'S-138°38'W, 660 m, fl., 21 July 1988 (BISH, P, PAP); *Gagné 1220*, Teauapuhiau Pass, above Ouia valley, 720 m, buds, 1-3 Aug. 1977 (BISH); *Wagner et al. 6152*, Ridge E of Mt. Teamotua from ridge below road along ridge to cascade, 640 m, fl., 21 July 1988 (BISH). ***Hiva Oa***: *Brown 1084A*, Feani, 900 m, st., 5 Apr. 1905 (BISH); *Chevrier in MacKee 44711*, Mokoau, 500 m, fr., 13 Nov. 1989 (P, PAP); *Decker 1189*, Puamau, along Puamau-Atuona trail, 500-650 m, fl., 14 Dec. 1963 (L, P, PAP); *Kondo s.n.*, Mt. Tapeata, 2500 ft., fr., 15 Oct. 1969 (BISH); *Mumford & Adamson 414*, Mt. Ootua, W slope, 700 m, buds, fr., 25 May 1929 (BISH); *Mumford & Adamson 497*, NW summit of Mt. Temetiu, 3400 ft., fl., fr., 3 Aug. 1929 (BISH); *Oliver & Schäfer 3216*, Mt. Ootua, old trail E of summit, 640 m, fr., 26 Feb. 1975 (BISH, PAP); *Perlman 10204*, trail towards Hanamenu, 3200 ft., juv., 3 Aug. 1988 (BISH, PAP); *Perlman 10259*, Vaipahee Falls rd., 1700 ft., fr., 10 Aug. 1988 (BISH, K, P); *Sachet & Decker 1903*, road from Atuona to Puamau, just below Mt. Ootua, 625-700 m, fr., 23 Nov. 1974 (P, PAP). ***Nuku Hiva***: *Florence 4303*, Toovii, épaulement au-dessus du réservoir, 8°52'S-140°09'W, 950 m, fr., 4 Dec. 1982 (BISH, P, PAP); *Florence 8421*, route Taiohae-Toovii, branche droite de la Ht. Taipivai, 8°53'S-140°08'W, 760 m, fl., 29 July 1987 (BISH, K, P, PAP); *Florence 4361*, route Toovii-Terre Déserte, km 6.8 après le col, 8°52'S-140°10'W, 960 m, fr., 9 Dec. 1982 (BISH, K, P, PAP); *Florence 8538*, Terre Déserte, crête Ouest du Mt. Akaupe, 8°52'S-140°10'W, 1180 m, buds, 10 Aug. 1987 (BISH, P, PAP); *Gagné 1033*, spur of Mt. Oomu, Toovii plateau, 790 m, fr., 16 July 1977 (BISH, L, P); *Gillett 2215*, Toovii-Taiohae trail, 2 km from

Tapuaooa shelter, 800 m, fr., 4 Aug. 1970 (BISH, K, L, P); *Lorence et al. 6089*, Toovii region, NW of l'Économic Rurale complex along new rd. to airport, 1060 m, fr., 16 July 1988 (P, PAP). ***Tahuata***: *Hallé 2168*, sommet, fl., fr., 17 Mar. 1973 (P); *Perlman et al. 14911*, summit of ridge above Vaitahu nr, Haaoiputeomo, nr. antenna, 2740 ft., fl., 1 Sep. 1995 (P); *Schäfer 5499*, Vaïtahu, crête d'Amatea, 620 m, st., 10 Apr. 1975 (K). ***Ua Huka***: *Florence 7262*, Hane, crête SW menant au Mt. Hitikau, 8°55'S-139°32'W, 540 m, fl., fr., 20 Feb. 1986 (P, PAP); *Quayle 1679*, s.loc., fr., 9 Nov. 1922 (BISH); *Quayle 1758* (BISH); *Quayle 1829*, fl. (BISH); *Quayle 1830*, fr. (BISH). ***Ua Pou***: *Quayle 1188*, fr., 12 Sep. 1922 (BISH).

LOCAL NAMES.—Atakua, Ata.

DISTINCTION FROM *WEINMANNIA PARVIFLORA*.—*Weinmannia marquesana* and *W. parviflora* are clearly closely related. Although BERNARDI (1964) regarded *W. marquesana* as distinct, FOSBERG & SACHET (1972) reduced it to a variety of *W. parviflora* (Table 1). We are once more giving it specific status although there is some overlap in characters (Table 2).

VARIATION WITHIN *WEINMANNIA MARQUESANA*.—This is a polymorphic species, varying in the size and shape of the leaves and the quantity and length of the indumentum, and thus it shows much the same range in variation as *Weinmannia parviflora*. Because of the range in amount and type of indumentum, we agree with BERNARDI (1964) that *W. marquesana* var. *glabrata* can not be maintained. However, one particularly distinctive variant originally named by FOSBERG & SACHET (1972) is maintained here, var. *myrsinites*. Because of the variability of this species, it is not surprising that there are some intermediates between the two named varieties (see below).

Florence 7262 is a specimen of *Weinmannia marquesana* var. *marquesana* from Ua Huka with female flowers, dehisced capsules and mostly trifoliolate leaves. In *W. parviflora* on Tahiti, occasional plants also occur with some trifoliolate leaves, either on the lower, sterile branches (e.g. *Hoogland & Florence 12911*) or on flowering branches (e.g. *Hoogland & Florence 12915*).

Florence 6882 from 1166 m on Nuku Hiva has a mixture of long and short, relatively thick and densely hairy internodes, and broadly elliptical or ovate leaves. It is thus vegetatively similar to collections of *Weinmannia parviflora* from high altitude on Tahiti. *Perlman et al. 14911* from Tahuata has exceptionally narrow leaflets.

TABLE 2.—Comparison of the characters of *Weinmannia parviflora* and *W. marquesana* var. *marquesana*

Character	*W. parviflora* (at low and mid elevation)	*W. marquesana* var. *marquesana*
Shape of leaf blade	narrowly elliptical	elliptical to ovate
length-breadth ratio excluding petiole	1: (0.27-)0.3-0.37(-0.47)	1: (0.36-)0.39-0.5(-0.58)
Stipules	persistent, recurved elliptical, spathulate or ± orbicular apex rounded, margin entire	caducous, often conduplicate broadly ovate apex acute, margin often toothed (sometimes narrowly ligulate with rounded apex and entire margin)
Capsules at dehiscence	2.5-3.5 mm long	3.3-5 mm long
Inflorescence	complex, racemes usually arising from 3 successive nodes, up to 11 racemes per inflorescence (pentad + 6)	simple, racemes arising usually at 1 node or sometimes 2, triad or pentad (rarely otherwise)
Indumentum on young stems	dense indumentum of erect hairs to 0.5 mm long	variable, dense to sparse

b. Weinmannia marquesana var. **myrsinites** (Fosberg & Sachet) H.C. Hopkins & J. Florence, **comb. nov.**

Weinmannia parviflora G. Forst. var. *myrsinites* Fosberg & Sachet, Micronesica 8: 45 (1972).—Type: *Sachet & Decker 1155*, Marquesas Islands, Hiva Oa, Atuona-Feani trail, 1200-1300 m, 24-26 Sep. 1963 (holo-, US!; iso-, BISH!, K!, L, NY, P!).

Shrub 0.6-1.5 m high, less commonly a small tree 2 m. Internodes usually short, ca. 0.5 cm long, nodes thickened, young stems strigose to puberulous. Leaves ovate or elliptical, the blade 1.6-2.7(-3.3) × 0.7-1.7 cm, plus a petiole 1-6 mm long, base cuneate or truncate, apex acute, blade coriaceous, the upper side drying dark purplish-brown, lower side dark chestnut, margin with 8-12 notches on either side, venation usually obscure and flat above, secondary and tertiary venation flat below and drying conspicuously darker than intervenium, bases of secondary veins frequently closer together in proximal part of blade, and basal veins more strongly arched towards apex than are the more distal ones, venation ± brochidodromus, reticulum of tertiary veins dense.—Fig. 4B, 5.

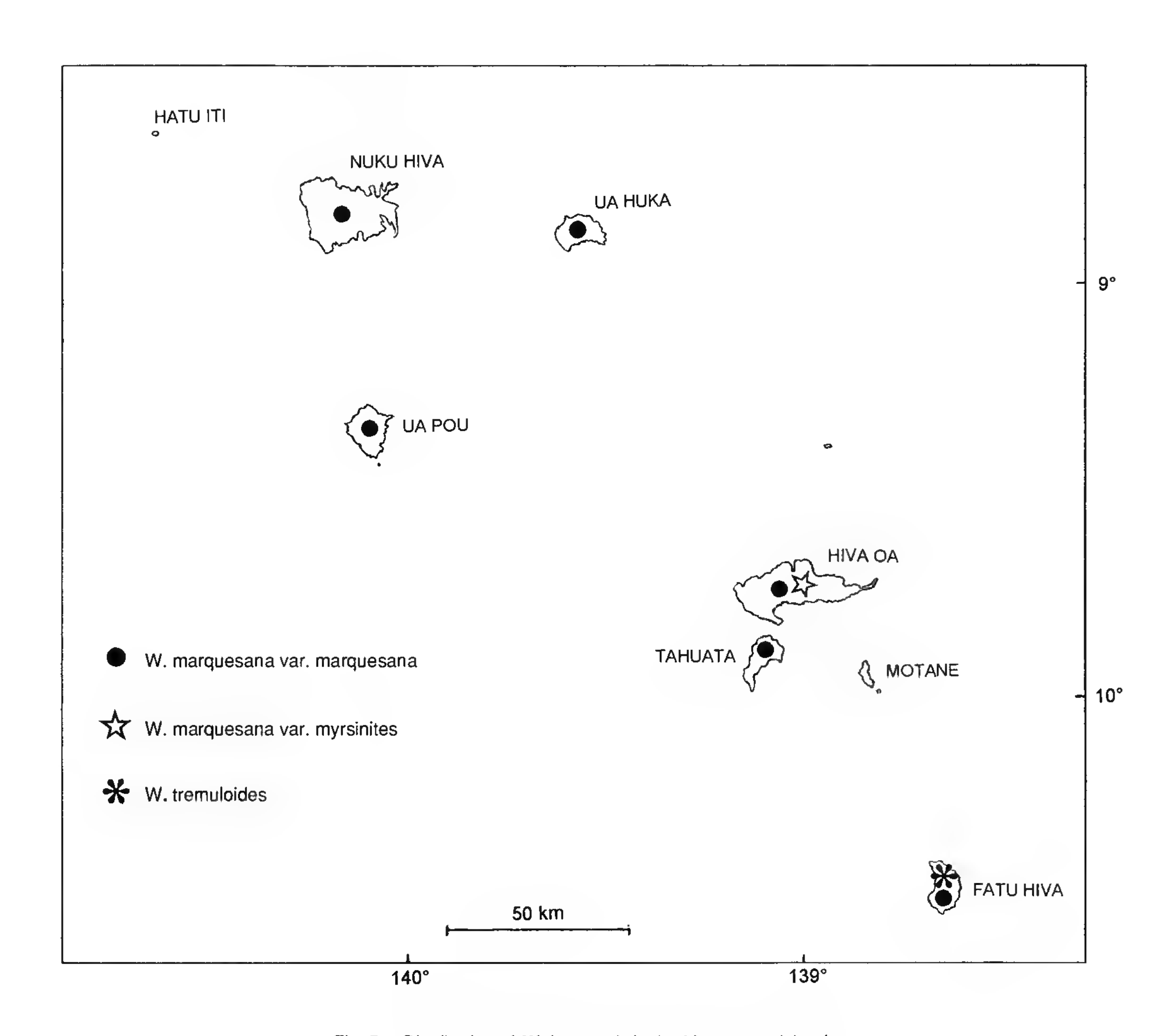


Fig. 5.—Distribution of ***Weinmannia*** in the Marquesas Islands.

Field characters.—The inflorescences are much shorter than in *W. marquesana* var. *marquesana*. Flowers white; young fruits red.

Distribution and ecology.—Marquesas: Hiva Oa, 800-1300 m. Common in scrub on upper, exposed, windswept slope at crest of ridge (maquis sommital) on dry side of island and also on leeward side in cloud forest.

Material examined.—Marquesas: ***Hiva Oa***: *Brown 1098*, Atuona, 800 m, st., Dec. 1921 (BISH); *Cherrier in MacKee 44689*, Feani, 1100 m, fl., fr., 11 Nov. 1989 (P, PAP); *Florence & Perlman 9667*, Atuona, piste de Hanameru, NW du Mt. Temetiu, 9°48'S-139°5'W, 1130 m, buds, fr., 30 July 1988 (BISH, K, P, PAP); *Oliver & Schäfer 3138*, Feani ridge, 1150 m, fr., 12 Feb. 1975 (BISH, PAP); *Oliver & Schäfer 3148*, ibid., 1050 m, fr., 12 Feb. 1975 (BISH, P); *Oliver & Schäfer 3155*, ibid., 1020 m, fr., 12 Feb. 1975 (BISH, P, PAP); *Perlman 10198*, trail towards Hanamenu, 3550 ft., buds, 3 Aug. 1988 (BISH, P, PAP).

Taxonomy and variation.—This variant of *Weinmannia marquesana* has a very distinctive morphology, and since names are often useful for such entities, we retain it as an infraspecific taxon. However, since it occurs only in more exposed situations, it may perhaps be no more than an ecotype of *Weinmannia marquesana*. A few collections from Hiva Oa have leaves that are either intermediate between the two varieties or have characteristics of both on same twig (*Oliver & Schäfer 3161*, *Perlman 10230*, *Sachet & Decker 1903*, *Decker 1189*). *Perlman 10130* (BISH, PAP) from Nuku Hiva has small leaves on stems with thickened internodes and dense erect hairs. Its venation is more similar to that of *W. marquesana* var. *marquesana* than var. *myrsinites* but the blades have dried almost black above and dark chestnut below. It is placed here with doubt.

5. Weinmannia tremuloides H.C. Hopkins & J. Florence, **sp. nov.**

Insignis inter omnes Gallicae Polynesiae species lateraliter complanato petiolo; a W. raiateensi J.W. Moore *longiore petiolo, angustioribus stipulis, majoribus fructibus, majoribus seminibus munitis longioribus pilis, praecipue differt.*

Type.—*Florence & Perlman 9581*, Marquesas Islands, Fatu Hiva, W ridge of Mt. Mounanui, 10°28'S-138°37'W, 700 m, buds, fr., 26 July 1988 (holo-, BISH!; iso-, CHR!, P!, PAP!, PTBG!, US!).

Shrub ca. 2 m high. Branching sometimes dichotomous. Stems finely longitudinally fissured, internodes 0.8-3 cm long, nodes somewhat thickened. Plant almost entirely glabrous, except for buds which have strigose hairs ca. 0.5 mm long, and occasional strigose hairs on young stems, stipules and leaves. Stipules oblong to ligulate, 0.6-0.8 × 0.2 cm, caducous. Leaves trifoliolate, total length up to 9 cm including petiole 2.5-4.2 cm; petiole laterally compressed and U-shaped in cross-section; leaflets narrowly elliptical, the lateral ones 3.6-4.4 × 0.7-1 cm, sessile and unequal at base, apex acute; terminal ones 4.8-6 × 0.8-1.1 cm, base attenuate, apex acute; the blade subcoriaceous, not punctate below, the margin somewhat thickened, crenate, 13-16 notches on each side of a lateral leaflet; midrib raised above, prominent below, secondary and tertiary venation somewhat indented above and flat below.

Inflorescence a central triad; peduncle and rachis segments glabrous; peduncle 1-1.7 cm long, rachis segments up to 6 cm long. Floral buds inserted singly; floral bracts ca. 1.1 mm long, ligulate, glabrous. Flowers at anthesis not seen. Calyx in bud glabrous.

Capsule 4-5 mm at dehiscence, the styles ca. 1 mm, exocarp sparsely hairy or ± glabrous; calyx lobes caducous, central column present. Seeds ca. 0.9 mm long, comose at both ends, the hairs 0.7 mm long.—Fig. 5, 6A-L.

Field characters.—The foliage has a trembling appearance because of the long, laterally compressed petioles. Flower buds white. Dehisced capsules brown.

Ecology and distribution.—Known only from Fatu Hiva where it was found in low vegetation on ridge top and cliffs with *Metrosideros*, *Dicranopteris* and *Lycopodium*, and described as abundant from 700-850 m.

Paratype.—Marquesas: ***Fatu Hiva***: *Perlman & Florence 10175*, slopes of Mounanui above Vaieenui Falls, 2300 ft., buds, 26 July 1988 (BISH).

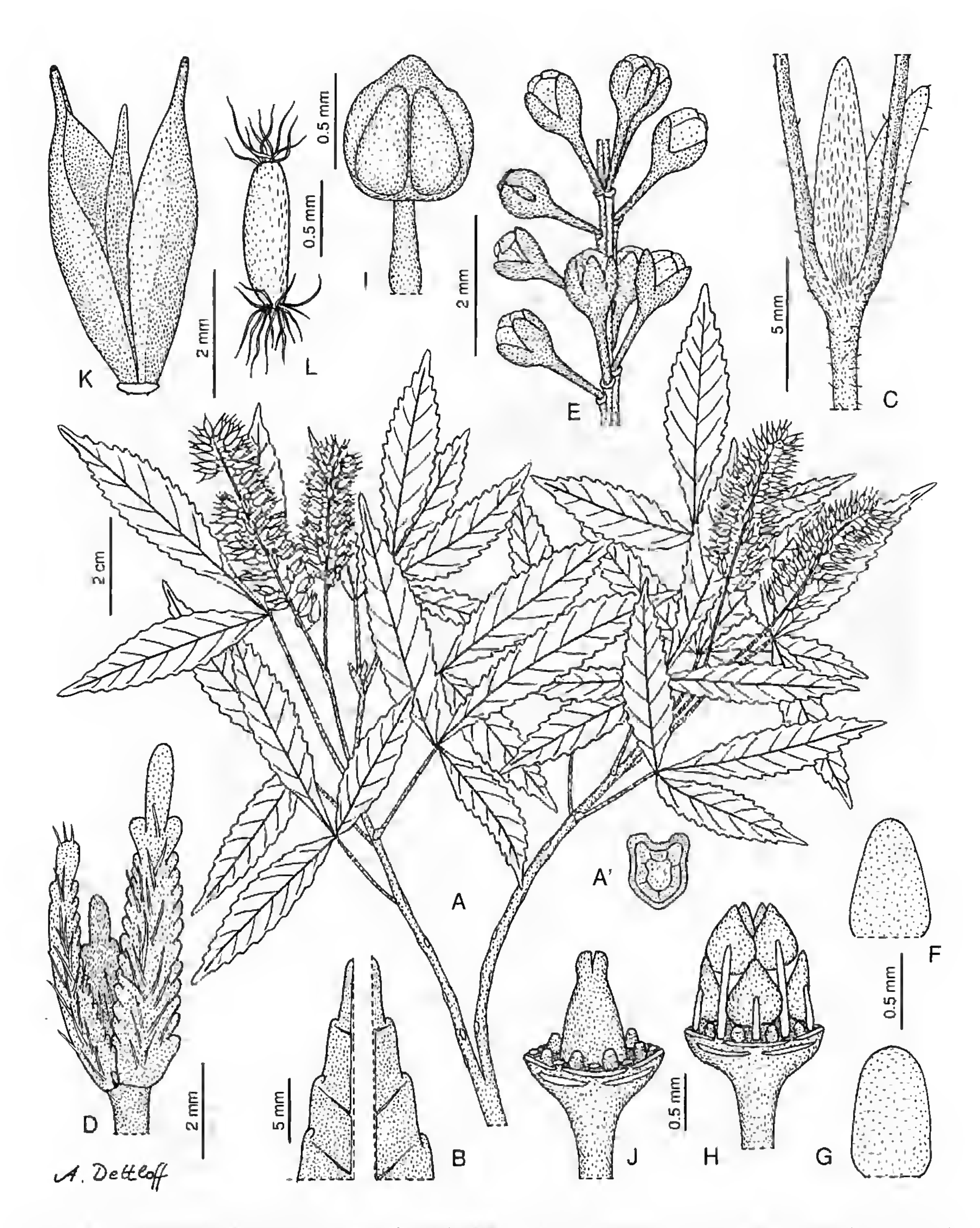


Fig. 6.—**A-L, *Weinmannia tremuloides***: **A**, fruiting shoot with trifoliolate leaves, the stipules caducous; **A'**, cross section of grooved petiole; **B**, summit of leaflet, above (left) and below (right); **C**, stipules; **D**, summit of young shoot showing developing leaves; **E**, detail of inflorescence, the buds inserted singly; **F**, sepal, outside; **G**, petal, outside; **H**, immature flower with calyx and corolla removed to reveal androecium; **I**, immature anther; **J**, immature flower with calyx, corolla and androecium removed to reveal developing gynoecium; **K**, dehisced fruit; **L**, seed. (A-L, *Florence & Perlman 9581*).—Drawn by A. DETTLOFF.

A well defined species. The leaflet shape is reminiscent of some specimens of *Weinmannia raiateensis* but the petiole is quite different. It is the most glabrous species in the region and the capsules are comparatively large, as in *W. marquesana*.

6. Weinmannia rapensis F. Br.

Bernice P. Bishop Mus. Bull. 130: 100 (1935); Bernardi, Bot. Jahrb. Syst. 83: 201, t. 35 (1964).—Type: *J. Stokes 306*, Rapa, Kulukulu [Kuluku in protologue] or Onape, 140 ft., 13 Oct. 1921 (holo-, BISH; iso-, BISH!).

Shrubby tree 1.5-6 m high, up to 20 cm dbh. Branching usually dichotomous with central bud aborted or if developed, then less strongly so than lateral shoots. Young stems densely pubescent, older ones minutely longitudinally fissured, sometimes lenticellate. Buds in leaf axils often prominent. Stipules usually caducous, rarely seen, ca. 0.9 × 0.6 cm at node subtending inflorescence, ± glabrous on adaxial surface, strigose on abaxial one, apex obtuse, up to 1.1 × 0.9 cm on vegetative shoots, margin toothed. Leaves compound, leaflets usually 3 or sometimes 5; petiole semiterete, 1-2.5 cm long, rachis segments in imparipinnate leaves 1.5-3 cm, petiole and rachis densely pubescent on flattened adaxial surface; lateral leaflets elliptical to narrowly ovate, 2.8-6.9 × 1.1-2.8 cm, base unequal to dimidiate, apex acute; apical leaflets elliptical or obovate, 4.2-10.3 (including petiolule up to 2 cm) × 1.7-3.5 cm, somewhat larger than lateral leaflets, base often strongly attenuate to form a petiolule, apex acute to acuminate; leaflet blades glabrescent except for midrib which is densely pubescent above towards base and strigose below, coriaceous, rarely punctate below; margin thickened, sometimes undulate, markedly crenate, crenations 14-26 down each side and strongly acroscopic; midrib slightly raised above and prominent below, secondary veins flat or slightly raised above and below.

Inflorescence either a central pentad, the lower racemes subtended by fully developed leaves, reduced leaves or neither, or a pair of pentads or triads, each developed from an axillary bud and the apical bud aborted. Inflorescence rachis segments 1-4 cm long, racemes up to 14 cm long. Auxiliary buds rarely seen, probably aborted. Stipules at nodes within inflorescence ovate, caducous, smaller than stipules at vegetative nodes. Floral buds inserted singly; floral bracts 1-2 mm long, caducous. Flowers male, female and bisexual; pedicel (1.3-)1.8-2.5 mm long, minutely hairy; calyx lobes shortly strigose or glabrous, sometimes warty, 0.9-1 mm long; petals oblong, 1.6-1.9 × 0.8-1 mm; filaments in male and bisexual flowers up to 2.5-3.5 mm long, in female flowers ca. 1.3-1.4 mm long, not always of equal length in any flower; disc lobes 0.5-0.7 mm long; ovary in male flowers 0.7-0.9 mm long plus styles 0.1 mm long, in female flowers 1.5-1.7 mm plus styles 1.2-1.5 mm long (at stage when anthers still present), variable in bisexual flowers according to age.

Capsules 2-3.5 mm at dehiscence, the styles 0.5-1 mm, exocarp glabrous with weak longitudinal ridges, sometimes warty, endocarp sometimes separating from the exocarp towards the apex; calyx lobes persistent or not, central column present. Seeds 0.7-0.8 mm long, comose at both ends.—Fig. 7A-E.

Breeding system.—Polygamodioecious. Different sheets of *St. John & Fosberg 15304* have male flowers and young fruits. *Hallé 7646* has morphologically male flowers in one inflorescence while another has bisexual ones. *A. Stokes 357* and *St. John & Maireau 15531* both have old female flowers.

Field characters.—Bark rough, dark brown, sapwood reddish brown (*St. John 15305*). Leaves bright green, coriaceous. Inflorescence rachis red, flowers white; petals almost white, anthers flesh-coloured, calyx and young capsules red; both male and female flowers reported as having a faint fragrance like *Ceanothus* (*St. John*).

Distribution.—Probably endemic to Rapa island.

Possible occurrence in the Pitcairn group.—Bernardi (1964: 202) records this species from the Pitcairn Group citing *Cuming 1428* (K) from Elizabeth Island, now Henderson Island, and *Cuming s.n.* (G) from "Pitcairn (?)". There are two sheets at Kew labelled *Cuming*

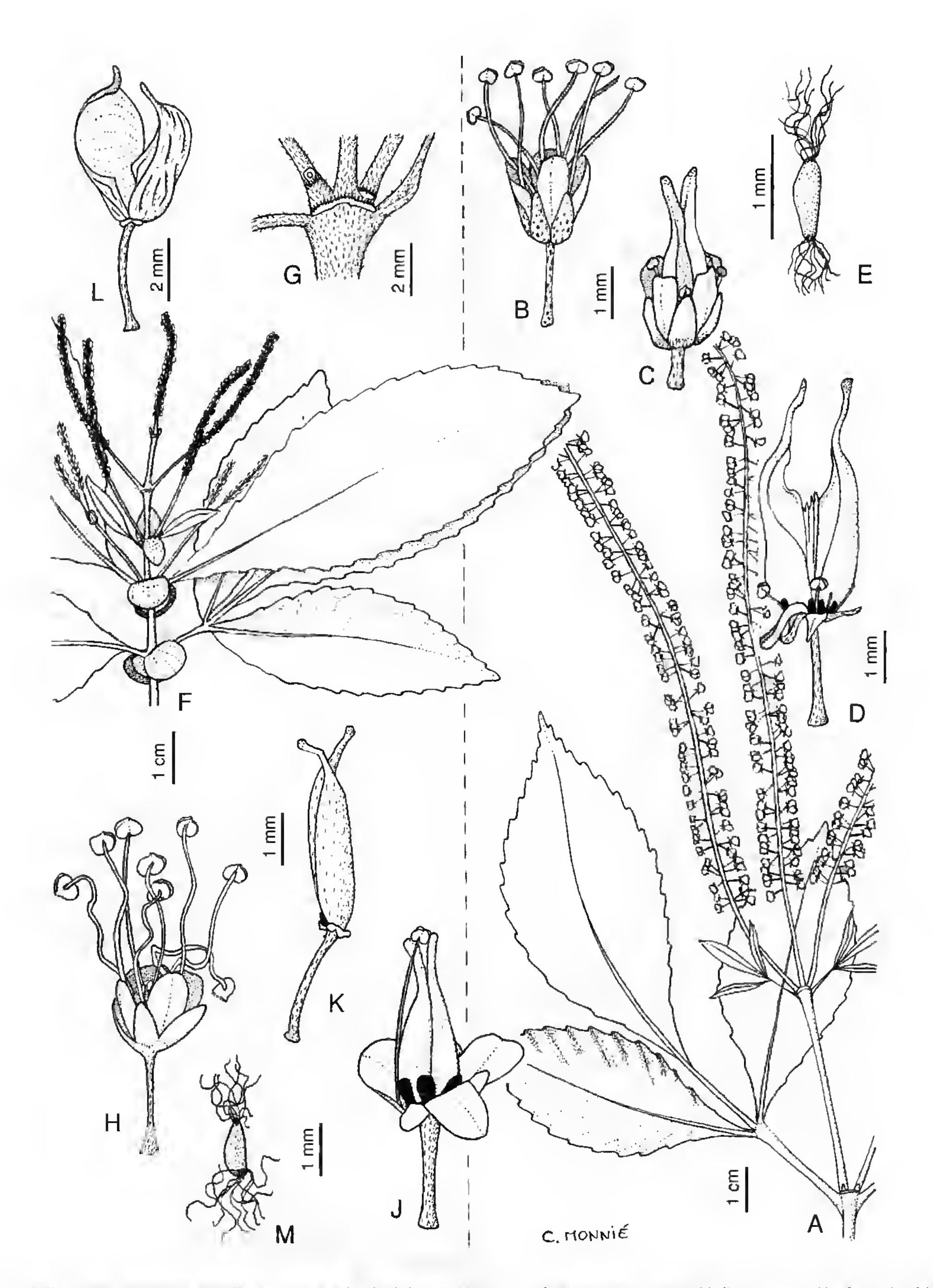


Fig. 7.—**A-E**, ***Weinmannia rapensis***: **A**, shoot with trifoliolate leaves, the stipules caducous and inflorescence (1 of a pair of lateral triads with a pair of reduced leaves at node); note lateral auxiliary buds at bases of peduncles; **B**, male flower; **C**, female flower; **D**, capsule at dehiscence; **E**, seed. (A, *Florence 6514*; B, D, E, *St. John & Fosberg 15304*; C, *Stokes 357*.—**F-M**, ***Weinmannia rarotongensis***: **F**, shoot with simple and trifoliolate leaves, persistent stipules with revolute margin and immature inflorescence (pentad); additional inflorescences also developing in the axils of more proximal leaves; **G**, detail of node showing opposite petioles and the peduncles of 3 partial inflorescences; note scars close to the base of the two lateral peduncles and row of colleters along stipular scar; **H**, male flower; **J**, female flower after anthesis, most of the stamens fallen; **K**, immature fruit; **L**, capsule at dehiscence; **M**, seed. (F, *Merlin 306*; G, K, *Parks 22522*; H, *MacKee 44309*; J, *Gardner 2503*; L, M, *Wilder 543*).—Drawn by C. Monnié.

1428. One gives the locality "Elizth Island" and the other "Ins. Toubouia". The record from Elizabeth Island is doubtful for several reasons. Firstly, according to ST. JOHN (1940) *Cuming 1428* was collected on Toubouia, now Tubuai Island in the Austral Group. Secondly, recent extensive botanical collections on Henderson Island, including the area where CUMING collected, failed to find this species (FLORENCE et al. 1995; S. WALDREN pers. comm.). Thirdly it is known that some of CUMING's labels became mixed up resulting in erroneous records (S. WALDREN pers. comm.). If *Cuming 1428* is from Tubuai, it is the first record from an island other that Rapa; CUMING visited both Tubuai and Rapa (ST. JOHN 1940: 88). The date of collection on one sheet is given as 1831 but 1828 is considered correct (ST. JOHN 1940).

ECOLOGY.—From 30-220 m. Reported from forest on steep slopes and crest of ridge, where *Metrosideros* is dominant and also from *Dicranopteris-Metrosideros* scrub on exposed slopes. Other associates include *Myoporum*, *Corokia* and *Fitchia*. Sometimes very abundant and forming thickets (*Hallé 7646*) but generally less common than is *Weinmannia parviflora* on Tahiti. Rapa island is colder and wetter than the Society and Marquesas Islands, since it lies farther south and its climate is influenced by cool, damp air currents from Antarctica (see PASTUREL 1993).

MATERIAL EXAMINED.—**AUSTRAL ISLANDS: *Rapa***: *Cuming 1428*, Rapa or Tubuai (K); *Florence 6395*, crête E vers Mt. Morongouta, 27°37'S-144°21'W, 210 m, fl., fr., 2 Feb. 1984 (BISH, K, P, PAP); *Florence 6514*, collines du NW de la baie de Haurei, 27°36'S-144°21'W, 50 m, fl., 6 Feb. 1984 (BISH, P, PAP); *Florence 6517*, S de Haurei, épaulement N du Mt. Maugaoa, 27°37'S-144°20'W, 75 m, fl., 7 Feb. 1984 (BISH, P, PAP); *Hallé 7501*, N vallée Hiri, 150 m, st., 2 Feb. 1984 (P); *Hallé 7517*, Morogo-Uta, 200-220 m, st., 2 Feb. 1984 (P); *Hallé 7646*, E du fond de la baie d'Ahurei, 30 m, fl., 6 Feb. 1984 (P); *Hallé 7700*, N de l'île Karapoo Rahi, fr., 9 Feb. 1984 (P); *Longfield 772*, s.loc., 11 Apr. 1925 (BM, K); *Paulay 29*, Maungaaiai, 250-350 m, 22 Jan. 1980 (A); *Raoul s.n.*, s.loc., fl. (P); *A. Stokes 2*, s.loc., 100 m, fl., 6 June 1921 (BISH); *A. Stokes 357*, Maungaaeae, 900 ft., fl., 19 Oct. 1921 (BISH); *St. John & Fosberg 15304*, Area, 75 m, fl., 1 July 1934 (A, BISH, L); *St. John & Fosberg 15305*, ibid., fl., fr., 1 July 1934 (A, BISH, K, L); *St. John & Maireau 15531*, Kaimaru, S ridge of Mt. Perahu, 400 m, fl., 13 July 1934 (BISH); *Varney 24*, piste de Hiri, 35 m, fl., 3 Jan. 1990 (P).

LOCAL NAME.—Aito. Local uses: fire wood and canoe parts (*A. Stokes 357*).

Rather uniform and distinctive. Most similar to *Weinmannia rarotongensis* (Fig. 7F-M), endemic to Rarotonga, the chief island of the Cook Islands, from which it differs by having uniformly trifoliolate leaves and being more velutinous on the stems and petioles. The branching is more often dichotomous and the crenation of the leaflet margins are more acroscopic. The stipules are usually caducous and not markedly recurved as in *W. rarotongensis*.

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INDEX TO TAXA AND SYNONYMS OF WEINMANNIA

This index includes all the taxa treated in the current revision of the Malesian-Pacific species (this paper and HOPKINS 1998a,b,c, all published in Adansonia, sér. 3, 20), thus some page numbers refer to the previous papers. Accepted names are in ordinary type, *synonyms* in italics, **new names** in bold, and invalid names in brackets. **F** = sect. *Fasciculata*, **L** = sect. *Leiospermum*.

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Landiopsis Capuron ex Bosser, genre nouveau de Rubiaceae de Madagascar

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MOTS CLÉS
Rubiaceae,
Landiopsis,
palynologie,
nouveau genre,
Madagascar.

RÉSUMÉ
Description de *Landiopsis* Capuron ex Bosser, genre nouveau de Rubiaceae-Cinchonoideae-Isertieae de Madagascar et de l'unique espèce connue : *L. capuronii* Bosser. L'étude palynologique confirme ses affinités avec le genre *Mussaenda*.

KEY WORDS
Rubiaceae,
Landiopsis,
palynology,
new genus,
Madagascar.

ABSTRACT
Description of *Landiopsis* Capuron ex Bosser, a new genus of Rubiaceae-Cinchonoideae-Isertieae from Madagascar and of *L. capuronii* Bosser, the only known species. Palynological study confirms its affinities with the genus *Mussaenda*.

CAPURON, à son décès en 1971, avait légué toutes ses notes et documents à Mme Françoise CHAUVET (CAPURON 1973). En ce qui concerne les Rubiaceae, les notes furent regroupées et dactylographiées en un seul document par Mme CHAUVET qui demanda à l'un de nous (J. BOSSER) de les revoir. CAPURON avait travaillé sur cette famille de longue date et il était évident qu'il n'aurait pas lui-même publié cette étude en l'état. Il fut donc décidé, en accord avec Mme CHAUVET, de tirer ce document en plusieurs exemplaires, afin que les chercheurs travaillant sur les Rubiaceae de Madagascar puissent y avoir accès. Ils furent déposés au CTFT (Paris, Tananarive) et un exemplaire fut confié au Professeur J.-F. LEROY du Laboratoire de Phanérogamie, Muséum de Paris. Ce dernier se chargea de l'étude de certains genres (*Mantalania*, *Pseudomantalania*) mais ne se pencha pas sur le cas du genre *Landiopsis*, proposé aussi par CAPURON, dont il nous remit récemment le matériel.

Il s'agit d'un arbuste du NW de Madagascar, sans raphides dans les tissus, à stipules interpétiolaires bifides ; inflorescences terminales cymeuses ; fleurs grandes ; calice à 5 lobes subulés ou, sur certaines fleurs, un des lobes développé en lame foliacée ; corolle longuement tubuleuse, à 5 lobes imbriqués ; étamines 5, incluses, subsessiles ; ovaire biloculaire, à 2 placentas axiles, multi-ovulés ; style court, à 2 branches stigmatiques cylindriques (des fleurs longistyles n'onr pas été observées) ; fruit capsulaire, déhiscent ; graines nombreuses, irrégulières, non ailées, finement ponctuées-réticulées.

LANDIOPSIS Capuron ex Bosser, **gen. nov.**

Mussaendae Burm. f. *atque* Pseudomussaendae Werhn. *affinis ; a primo aestivatione imbricata et fructu capsulari, a secundo aestivatione imbricata, praecipue differt.*

TYPE. — *Landiopsis capuronii* Bosser.

Le nom *Landiopsis* est basé sur *Landia* proposé par COMMERSON et repris par POIRET pour un *Mussaenda* des Mascareignes.

Landiopsis capuronii Bosser, **sp. nov.**

Frutex sine raphidibus, 4-5 metralis. Inflorescentiae terminales, cymosae. Flores 5-meri, magni. Calycis lobis linearibus, uno aliquando foliaceo. Corolla lobis patentibus, imbricaris ; tubo cylindrico. Stamina 5, subsessilia, inclusa, infra corollae orem affixa. Ovarium biloculare ; placentis axialibus, multiovulatisque ; stylus inclusus, brevisque, stamina haud attingens. Discus annularis. Capsula septicidalis. Semina multa minutaque, plusminusve reniformia, exalata ; testa subtiliter reticulata.

TYPE. — *Service Forestier 24467-SF, Capuron*, Madagascar, 3 fév. 1966 (holo-, P ; iso-, B, BR, G, K, MO, P, PRE, TEF, WAG).

Arbuste atteignant 4-5 m de hauteur, sans raphides dans les tissus ; rameaux jeunes densément pileux, poils hirsutes, atteignant 1 mm de longueur ; rameaux âgés ± glabrescents, brunâtres, à lenticelles allongées plus claires. Feuilles opposées, caduques, membraneuses, discolores, à face inférieure plus pâle ; limbe plan, enrier, ovale ou elliptique à largemenr ovale ou largemenr elliptique, cuspidé au sommet, cunéiforme à la base, un peu dissymétrique et décurrent sur le pétiole, 5-10 × 2,5-6 cm ; faces supérieure er inférieure pubescentes, à poils situés sur les nervures et les nervilles ; réseau des nervilles noirâtre, ressortant sur le fond plus clair ; pétioles grêles, densément pubescents, longs de 6-18 mm. Stipules interpétiolaires, longues de 6-7 mm, bifides, chaque lobe prolongé en arête très fragile, pubescentes sur les 2 faces, finalement fendues jusqu'à la base, ayant à leur aisselle une ligne très dense de poils blancs. Inflorescences terminales, 3-15-flores, en cymes dichotomes assez denses, sessiles, les 2 premières ramifications partant de la base ; cymules pédonculées, les pédoncules densément pubescents, longs de ± 5 mm ; bractéoles 2, longues de ± 1 cm, linéaires, parfois tri-aristées avec 2 arêtes latérales beaucoup plus courtes, ayant à leur aiselle un groupe d'arêtes plus courtes représentant une fleur avortée. Fleurs grandes, blanches, 5-mères, sessiles ou courtement pédicellées. Calice à 5 lobes subulés pubescents-hirsures, un peu soudés à la base, longs de 0,7-1,8 cm ou, plus souvent, 1 des lobes beaucoup plus grand et développé en lame foliacée, pétiolée, blanche, pubescente puis ± glabrescente, lancéolée ou étroitement elliptique, aiguë, 2-3 × 0,8-1,2 cm, devenant scarieuse sur le fruit, à pétiole long de ± 1,5 cm, pubescent. Corolle tubuleuse, longue de 5-6,5 cm ; tube long de 3,5-5 cm, cylindrique sur les 2/3 inférieurs et de 2-2,5 mm de diamètre, dilaté au niveau des anthères et de 4 mm de diamètre, extérieurement à pubescence dense, antrorse, apprimée, blanche, intérieurement à pubescence hérissée, clairsemée, sous la zone d'insertion des étamines ; lobes 5, imbriqués, lancéolés ou étroitement elliptiques, aigus, finalement étalés, 10-12 × 5-7 mm, pubescents sur les 2 faces, les nervures médianes saillantes à la base du côté interne, se rejoignant et fermant la gorge. Étamines 5, incluses, insérées au 1/4 supérieur du tube de la corolle ; anthères étroitement oblongues, apiculées au sommet, bilobulées à la base, vert olive, à déhiscence introrse, subbasifixes, subsessiles l'extrémité du filet ± soudé au tube, longues de 4,5-5 mm. Pollen en grains simples tricolporé. Ovaire obconique, environ 5 × 2 mm, pubescent-blanchâtre, biloculaire, à placentation axile, chaque loge

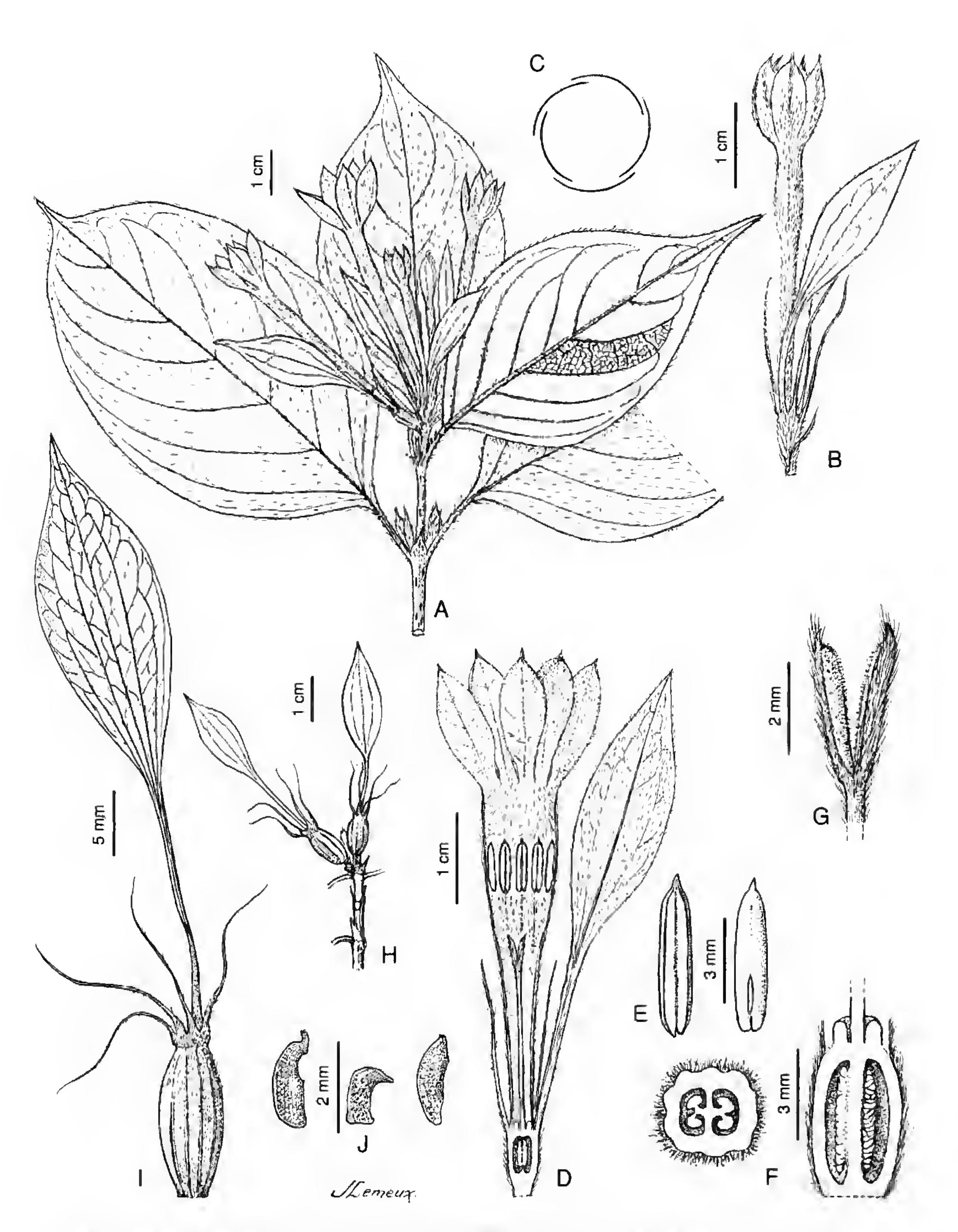


Fig. 1. — ***Landiopsis capuronii*** : **A**, rameau fleuri ; **B**, bouton floral ; **C**, diagramme de la préfloraison ; **D**, coupe longitudinale d'une fleur ; **E**, anthère, de face et de dos ; **F**, coupe transversale et longitudinale de l'ovaire ; **G**, stigmates ; **H**, rameau fructifère ; **I**, fruit ; **J**, trois formes de graines. [A-G, *24467-SF, Capuron* (P) ; H-I, *24668-SF, Capuron* (P)].

contenant un placenta allongé fixé sur toute sa longueur ; en coupe transversale, placentas en forme de T, les ovules étant fixés aux extrémités des branches du T ; ovules très nombreux, horizontaux ; style inclus, long de 2,5-3 cm, glabre, divisé au sommet en 2 branches stigmatiques longues de ± 2,5 mm, apiculées, pubescentes sur le dos et papilleuses sur la face interne ; stigmate situé sous la zone d'insertion des anthères ; disque présent, haut d'environ 0,5 mm, entourant la base du style. Fruit, capsule à déhiscence septicide, ovoïde ou ellipsoïde, 8-10 × 5-6 mm, pubescente, faiblement côtelée, portant quelques lenticelles blanchâtres saillantes ; calice persistant mais non accrescent. La capsule finalement se déchirant en 4 valves, l'exocarpe se détachant de l'endocarpe. Graines nombreuses, très petites, d'environ 1,5-2 × 1 mm, non ailées, ± réniformes, irrégulières, comprimées latéralement, à tégument finement réticulé. — Fig. 1.

Espèce de la forêt décidue sèche du Nord-Ouest de Madagascar, rare, connue seulement par 2 récoltes.

MATÉRIEL ÉTUDIÉ. — MADAGASCAR : *Service Forestier 24467-SF, Capuron*, NW, massif de l'Ankotekona, au S de la baie d'Ambararata (Diego-Suarez), alt. 150 m, 3 fév. 1966, fl., type (B, BR, G, K, MO, P, PRE, TEF, WAG) ; *Service Forestier 24668-SF, Capuron*, même localité, entre 25 et 265 m d'alt., 25 avr. 1966, fr. (BR, G, K, MO, P, TEF, WAG).

Par le port, les grandes fleurs, les caractères séminaux, cette plante rappelle certains *Mussaenda* (Isertieae) comme le *M. landia* Poir. des îles Mascareignes. Cependant, l'association des 2 caractères : corolle à préfloraison imbriquée et fruit capsulaire déhiscent, semblait la rapprocher de la tribu des Rondeletieae.

Pour tenter de préciser la position de ce genre, l'un de nous (D. LOBREAU-CALLEN) en a entrepris l'étude palynologique.

Morphologie du pollen

Le pollen des Rubiaceae a fait l'objet de nombreuses publications (THANIKAIMONI 1972-1986 ; TISSOT 1990 ; TISSOT & VAN DER HAM 1994). Dans plusieurs espèces, il présente un caractère apertural rare chez les Eudicotylédones (LOBREAU-CALLEN 1978) : l'aperture composée des grains colporés ou pororés est constituée de 3 parties, une ectoaperture avec une membrane souvent granuleuse, une mésoaperture circulaire entourée d'un annulus de foot-layer et une endoaperture circulaire ou elliptique située dans l'endexine (LOBREAU-CALLEN 1978 ; VASANTHY 1978 ; ANDERSSON & PERSSON 1991 ; PERSSON 1993 ; PUFF et al. 1993 ; HUYSMANS et al. 1994). Ce type pollinique est dérivé d'un pollen tricolporé formé de 2 parties, une ecto- et une endoaperture (LOBREAU-CALLEN 1978). Le grand développement de l'annulus et l'augmentation du nombre des apertures sont aussi considérés comme des caractères évolués (ROBBRECHT & PUFF 1986 ; ANDERSSON & PERSSON 1991).

Le pollen de *Landiopsis* a été comparé au pollen d'espèces appartenant à la tribu des Isertieae : *Isertia coccinea* (Aubl.) Gmel. [*de Granville 64*, Aratayc, Guyane (P)] ; *Mussaenda frondosa* L. [*Balansa 625*, Tonkin, Viet-Nam (P)] ; *M. landia* Poir. [*Friedmann 463*, La Réunion (P)] ; et à la tribu des Rondeletieae : *Rondeletia bourgaei* Standl. [*Botteri 1016*, Mexique (P)] ; *R. buddleioides* Benth. [*Galeotti 2682H*, Yotao, Mexique (P)].

Les pollens ont été acétolysés et observés au Mph sur un appareil Zeiss standard et au MeB sur un microscope Jéol 840A après métallisation à l'or-palladium.

Le pollen de *Landiopsis* (Fig. 2A-D) est bréviaxe, isopolaire et brévi-tricolporé (Fig. 2A). L'aperture est complexe et constituée de 3 parties :
- — une ectoaperture large, courte et arrondie aux extrémités, plus développée vers l'un des pôles et recouverte d'une membrane scabre (Fig. 2B) ;
- — une mésoaperture circulaire, entourée d'un annulus (Fig. 2C) ;
- — une endoaperture elliptique, allongée sur l'équateur (Fig. 2C).

L'exine massive (Fig. 2D) est formée par un tec-

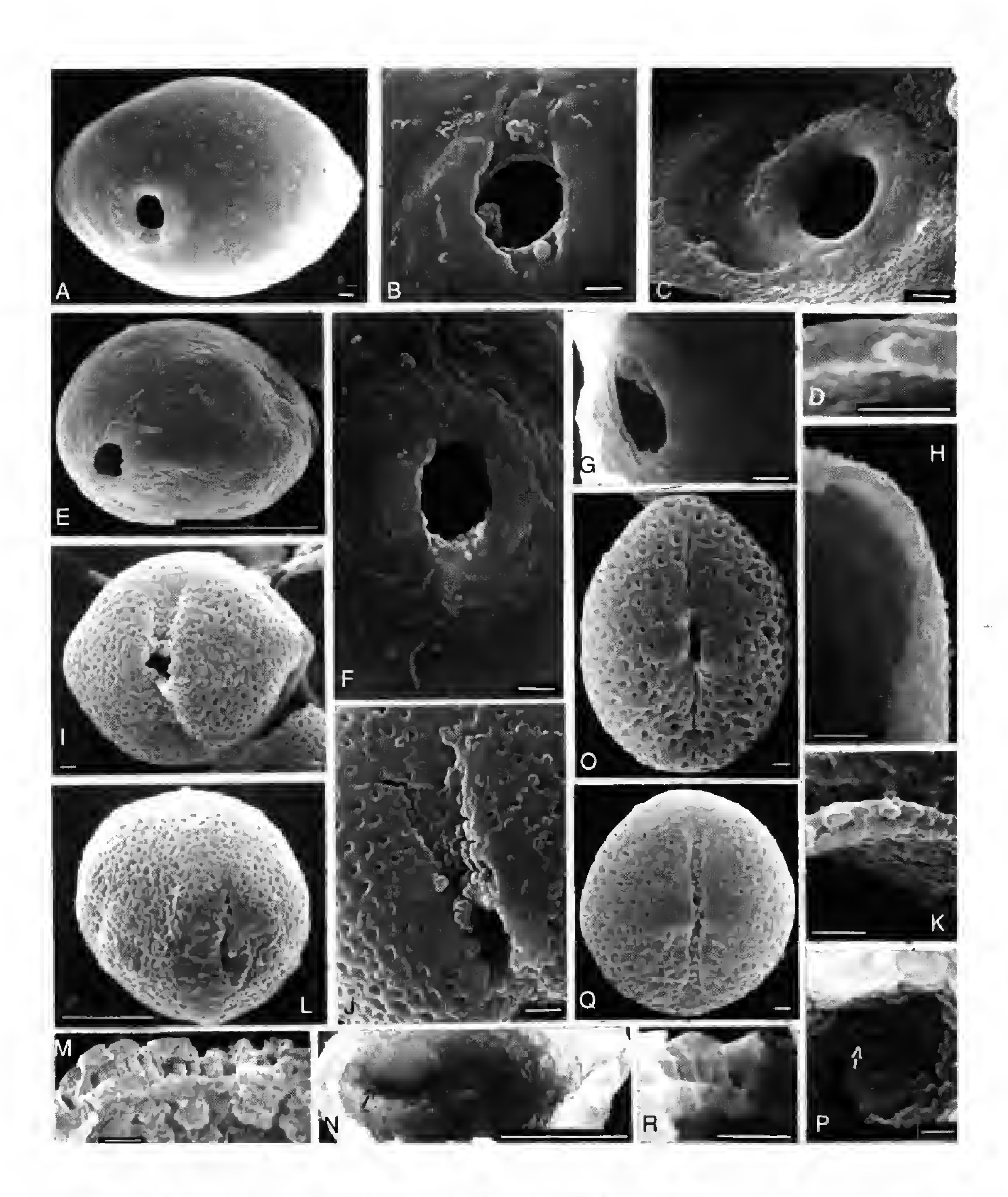


Fig. 2. — A-D, ***Landiopsis capuronii*** ; E-H, ***Mussaenda landia*** ; I-K, ***M. frondosa*** ; L-N, ***Isertia coccinea*** ; O-P, ***Rondeletia bourgaei*** ; Q-R, ***R. buddleioides*** : **A, E, L, O, Q**, pollen tricolporé ; **B, F, J**, ectoaperture ; **C, G**, endoaperture et mésoaperture entourée d'un annulus ; **D, H**, structure massive de l'exine ; **I**, pollen tétracolporé ; **K**, exine avec de très courtes columelles ; **M**, infratectum columellaire et nexine endocraquelée ; **N, P**, endoaperture subrectangulaire et nexine endocraquelée ; **R**, infratectum columellaire et nexine endocraquelée. (Échelle : A-D, F-K, M, O-R = 1 µm ; E, L, N = 10 µm).

TABLEAU 1. — Comparaison des caractères polliniques de *Landiopsis* et des trois genres proches.

CARACTÈRES POLLINIQUES	*Landiopsis*	*Mussaenda*	*Isertia*	*Rondeletia*
SYMÉTRIE	± isopolaire	± isopolaire	± isopolaire	isopolaire
APERTURES (nombre)	3	3-4	3	3
ECTOAPERTURE	courte, large, parfois dissymétrique	longue, symétrique ou non, parfois à peine distincte	courte et étroite, parfois dissymétrique	longue et étroite
extrémités	arrondies	aiguës ou dichotomiques	aiguës	aiguës
membrane	lisse ou scabre	granuleuse	granuleuse	granuleuse
MÉSOAPERTURE	circulaire	circulaire	absente	absente
annulus	net	net	absent	absent
ENDOAPERTURE	elliptique	circulaire	subrectangulaire	subrectangulaire
TECTUM	lisse	perforé ou fovéolé	perforé	perforé
INFRATECTUM	indistinct	columellaire ou indistinct	columellaire	columellaire
NEXINE	micro-endosculptée	micro-endosculptée	endocraquelée	endocraquelée

tum lisse, un infratectum de structure indistincte au Mph comme au MeB, et une nexine finement endosculptée.

Par ses caractères macromorphologiques, le pollen de *Landiopsis* a des affinités avec celui des Isertieae et des Rondeletieae. Chez les Isertieae, PUFF et al. (1993), ANDERSSON (1996) et HUYSMANS et al. (comm. pers.) ont étudié le pollen de l'ensemble des genres du groupe. Les grains sont 3(-4) colporés et le tectum est perforé, « fovéolé », ou réticulé ; l'infratectum est columellaire, rarement de structure indistincte (*Isertia* p.p.). Le pollen d'*Isertia* diffère de celui des autres genres par son sillon court et relativement indistinct alors que celui de *Mussaenda* se caractérise par un sillon généralement tronqué aux extrémités et par un annulus autour de l'endoaperture. Le pollen des Rondeletieae est tricolporé et le tectum nettement perforé (BORHIDI 1982 ; BORHIDI & JARAI-KOMLODI 1983 ; IGERSHEIM 1993).

Dans l'étude que nous avons faite, seul le pollen de *Mussaenda* tri- ou tétracolporé (Fig. 2E,I) présente une aperture formée de 3 parties dont une ectoaperture longue (Fig. 2F,J), une mésoaperture circulaire entourée d'un annulus (Fig. 2G) et une endoaperture concentrique. Le pollen de *Mussaenda* rappelle donc celui de *Landiopsis*. Cependant, chez *Mussaenda*, la membrane aperturale est granuleuse (Fig. 2F,J) alors qu'elle est scabre chez *Landiopsis*. En revanche, dans les deux genres *Isertia* et *Rondeletia*, le pollen est tricolporé (Fig. 2L,O,Q) et l'aperture ne comprend que 2 parties : une ectoaperture allongée, courte lorsque les grains sont bréviaxes (*Isertia*, Fig. 2L) ou longue lorsqu'ils sont longiaxes (*Rondeletia*) et, dans tous les cas, une endoaperture subrectangulaire (Fig. 2N,P).

Dans tous les genres, le pollen est tecté, régulièrement perforé, parfois finement (*Isertia*, *Mussaenda*) (Fig. 1I,L,O,Q) et l'infratectum est distinctement columellaire (Fig. 1K,M,R). Plus rarement, le tectum est lisse, à peine perforé et fossulé (Fig. E) et la structure de l'infratectum est indistincte (Fig. 1H). Ainsi, par les caractères de la sexine, le pollen de *Landiopsis* montre des affinités avec ceux de *Mussaenda* et d'*Isertia*.

Chez les Rubiaceae, la nexine peut être lisse, endosculptée ou moins fréquemment endocraquelée et alors formée de plaques dans sa partie profonde (ABABIE & KEDDAM-MALPLANCHE 1975 ; HUYSMANS et al., comm. pers.). Ce caractère se retrouve chez *Isertia* et *Rondeletia* où il est particulièrement net (Fig. 2M,N,P,R). En revanche, cette même couche est micro-endosculptée chez *Mussaenda* (Fig. 2H,K) comme chez *Landiopsis*.

En conclusion (Tableau 1), le pollen de *Landiopsis* est original par sa membrane aperturale lisse. Cependant, il présente des affinités évidentes avec celui de *Mussaenda* puisqu'ils ont en commun le même système apertural et la nexine micro-endosculptée.

Par les caractères principaux des stipules, de l'inflorescence, de la fleur, du fruit et de la graine, le genre *Landiopsis* fait partie de la tribu des Isertieae telle qu'elle a été circonscrite par ANDERSSON (1996).

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A floristic inventory and preliminary vegetation classification of the mixed semi-evergreen rain forest in the Minkébé region, North East Gabon

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KEY WORDS
Floristic inventory,
Minkébé,
Gabon,
rain forest,
Gilbertiodendron.

ABSTRACT
This study describes the flotistic diversity and vegetation of the Minkébé area in North East Gabon, an area hitherto poorly known. A total area of 290 ha was completely surveyed for trees > 70 cm dbh. A detailed inventory for trees > 10 cm dbh of a 3 ha plot was conducted. Many new records could be added to the existing checklist. Spatial distribution of the major species is presented as well as a preliminary vegetation typology. Attention is given to the ecological and successional status of the tree species with special emphasis on *Gilbertiodendron dewevrei.* Comparisons are made with data on forest composition in Gabon from various authors.

MOTS CLÉS
Inventaire floristique,
Minkébé,
Gabon,
forêt ombrophile,
Gilbertiodendron.

RÉSUMÉ
La diversité floristique et la végétation de la région de Minkébé au Nord-Est du Gabon, une région très peu connue jusqu'à maintenant, sont étudiées. Une surface totale de 290 ha a été complètement explorée pour des arbres > 70 cm dbh. Un inventaire détaillé des arbres > 10 cm dbh a été également réalisé sur une surface de 3 ha. Beaucoup d'espèces ont été ajoutées à la liste systématique existante. La distribution spatiale des espèces dominantes est présentée, de même qu'une typologie préliminaire de la végétation. La position écologique et sylvigénétique des espèces arborescentes est signalée en accordant une attention spéciale à *Gilbertiodendron dewevrei.* Des comparaisons sont effectuées avec les données fournies par plusieurs autres études traitant de la composition forestière au Gabon.

INTRODUCTION

This paper presents part of the results of the floristic and vegetation inventories of a multi-disciplinary study in the Minkébé area, North East Gabon, within the framework of the WWF program for Gabon.

Information on the vegetation of North East Gabon is rather scarce. According to WHITE (1983) the forests of Gabon are part of the Guineo-Congolian regional centre of endemism. The forest in the North East of Gabon belongs to the mixed moist semi-evergreen Guineo-Congolian forest type (WHITE 1983). Though the prevalent vegetation is moist semi-evergreen forest of mixed composition, small islands of single-dominant forest are also found scattered throughout. The upper stratum of single-dominant forest is uniform and dense, usually 35-45 m high and is composed of a single or very few species.

According to CABALLÉ (1978) two vegetarion types can be distinguished in eastern Gabon. The first one called "forêt dense à tendance semi-caducifoliée" with *Pycnanthus angolensis*, *Pentaclethra eetveldeana*, *Terminalia superba* and *Triplochiton scleroxylon*. The second type called "forêt dense humide sempervirente" with *Scyphocephalum ochocoa*, *Pycnanthus angolensis*, *Pentaclethra eetveldeana*, *Celtis spp.*, *Gilletiodendron pierreanum* and *Gilbertiodendron dewevrei*. The last species forms single-dominant forest islands. The quanrirative importance of Burseraceae, Irvingiaceae, and Olacaceae is far less than in the west of the country (e.g. absence of okoumé, *Aucoumea klaineana*), whereas rhe importance of Mimosaceae and Papilionaceae increases towards the east of Gabon.

In 1966 a forest inventory was carried our in the Bélinga mountains 50 km southeasr of the Minkébé area (AUBRÉVILLE 1967; HALLÉ et al. 1967). REITSMA (1988) gives a derailed quantirative ecological inventory of four one-hecrare plots of undisturbed lowland forest in Gabon. One of his plots is located at Ekobakoba, south of Bélinga and southeast of Makoukou (Fig. 1). Floristically Notth Easr Gabon has been described in 6 checklists (HALLÉ 1964, 1965; HALLÉ & LE THOMAS 1967, 1970; HLADIK & HALLÉ 1973; FLORENCE & HLADIK 1980).

METHODS

FIELDWORK

The basecamp was situated on a high bank of the Sing river, at 1°30'N, 12°48'E. A line survey was conducted with an orientation of 80 grads and 280 grads (Fig. 1). Within the transect two surveys were carried out, one of trees > 70 cm dbh (diameter at breast height measured at 1.3 m above ground or immediately above the buttresses if these extend beyond 1.3 m) and a second concerning trees > 10 cm dbh. The fieldwork was carried out in 1990.

The survey of rrees > 70 cm dbh comprised an area with a rotal length of 58 km and was 50 m wide (surface area 290 ha), divided into 500 × 50 m sections. The location of every tree > 70 cm dbh was mapped, the diameter measured and if neccesary a voucher specimen was collected for identification.

The survey of trees > 10 cm dbh comprised a transect of 6 km length and was 5 m wide (surface area 3 ha), divided in 100 × 5 m sections. The locality of every tree > 10 cm dbh was mapped, the diameter measured and if neccesary a voucher specimen was collected for idenrification. In addition also all plants, including herbs and shrubs, beating flowers and/or fruits ptesenr on the transect wete collected to get an impression of the floristic divetsity. An additional florisric survey was carried out along rivets and streams.

DATA PROCESSING

The voucher specimens and a complete set of all fertile herbarium specimens were sent to Wageningen (Herbarium Vadense) for identificarion. The fitst ser of ferrile herbarium specimens is present at the Herbier National CENAREST, Libreville. A complete listing of the species can be found in VAN VALKENBURG (1990) and in STEEL (1992).

For all species found a diameter class disttibution was made and the location of main species along the ttansect drawn on scale.

In ordet to asctibe an importtance value to a family or species the relative frequency of that family or species was determined by the following formula.

$$\text{Relative frequency} = \frac{\text{number of individuals of a taxon}}{\text{total number of individuals}} \times 100\%$$

The quantitative data gathered in the vegetation survey were used for a preliminary classification of the forest vegetation. For the vegetation analysis each section was treated as a relevé. Not only the absence or presence of species was taken into account but also the abundance. The number of individuals was transfered into the following classes: absent = –, 1-2 trees = 1, 3-4 trees = 2, 5-6 trees = 3, 7-8 trees = 4, > 8 trees = 5.

These data were processed using a computer cluster programme TWINSPAN (Hill 1979) and adapted by the former Department of Vegetation Science, Plant Ecology and Weed Science. Twinspan is a polythetic divisive cluster programme. The polythetic method means that divisions are made based upon all species present in the relevés, and the abundance of species is also taken into account. The resulting clusters were analysed and interpreted before well defined vegetation types could be distinguished. With the computer programme Clutab, a synoptic table was prepared, giving frequencies on a scale of 5 of each species per cluster.

After a typology of the vegetation of the 500 m as well as the 100 m plots was made, the large and the small plots were combined and compared. Using field observations, the data on diameter distribution of the various tree species,

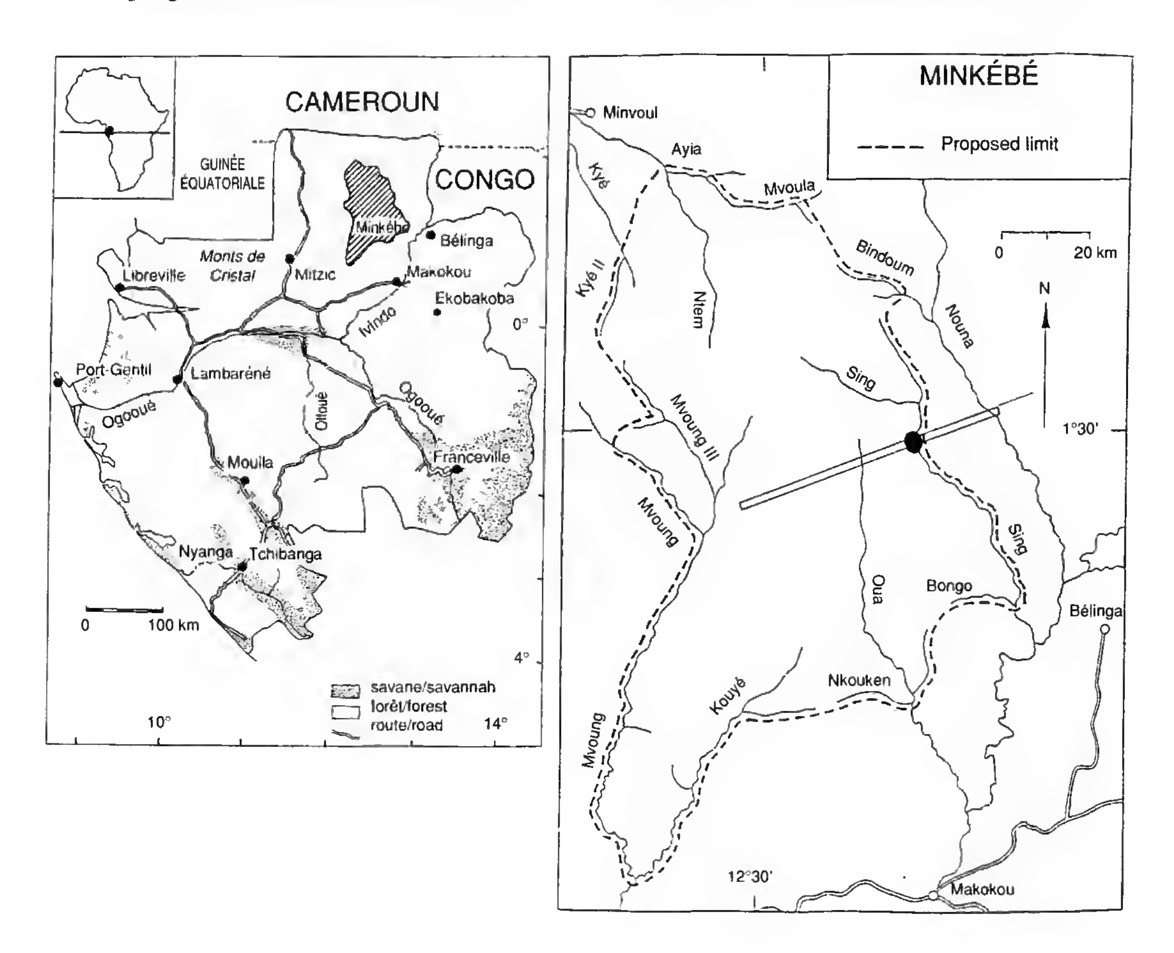


Fig. 1.—Map of Gabon with the location of the various research sites (adapted from Reitsma 1988).

diameter distribution within plots, scarce data from literature about ecological requirements of certain tree species (e.g., CABALLÉ 1978; GÉRARD 1960; SAINT AUBIN 1963; WHITE & ABERNATHY 1996) and their status in the successional process, insight in the forest dynamics was attempted.

RESULTS

FLORISTIC DIVERSITY

The floristic survey of the two transects in the Minkébé area, including riversides and a general collecting of flowering and/or fruiting plants, resulted in 655 taxa identified to species level in 89 families (VAN VALKENBURG 1990; STEEL 1992). Many specimens could only be identified to genus or family level; 214 new taxa could be added to the existing checklist for North East Gabon (HALLÉ 1964, 1965; HALLÉ & LE THOMAS 1967, 1970; HLADIK & HALLÉ 1973; FLORENCE & HLADIK 1980). An additional collecting trip in December 1990 has added another 3 species to this list of new records, although still a considerable number of specimens has to be identified (Appendix 1).

The survey of trees > 70 cm dbh (totalling 290 ha) comprised a total of 1148 individuals of 113 species in 34 families. The three most important families are Caesalpiniaceae (27,1%), Mimosaceae (20,9%), Burseraceae (7%).—Fig. 2. The ten most common species are *Dacryodes buettneri*, *Distemonanthus benthamianus*, *Erythrophleum ivorense*, *Gilbertiodendron dewevrei*, *Monopetalanthus pellegrinii*, *Cylicodiscus gabunensis*, *Pentaclethra eetveldeana*, *Piptadeniastrum africanum*, *Pycnanthus angolensis*, and *Pterocarpus soyauxii*, followed by *Alstonia boonei*, *Terminalia superba*, and *Petersianthus macrocarpus*.

The survey of trees > 10 cm dbh (totalling 3 ha) comprised a total of 1155 individuals of 202 species in 45 families. The three most important families are Caesalpiniaceae (28.7%),

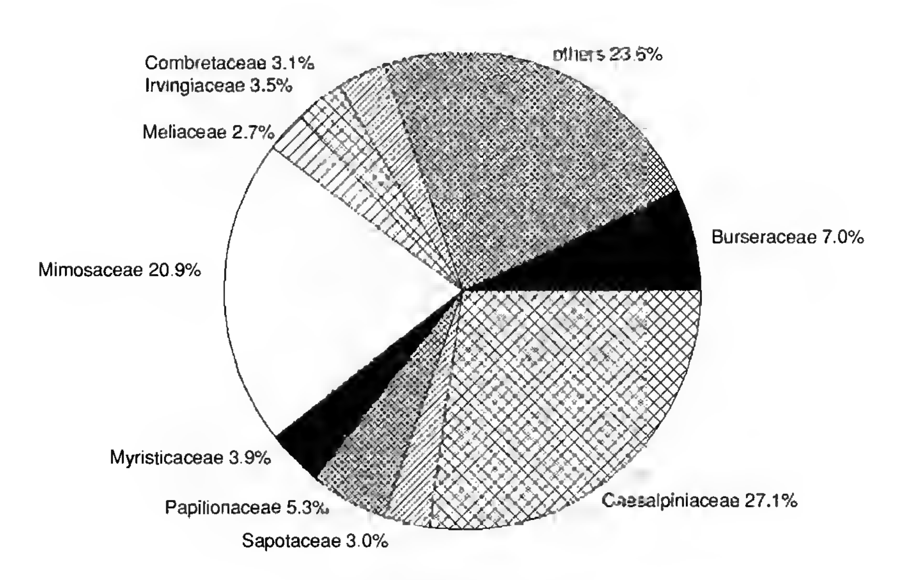


Fig. 2.—Family importance (as percentage of total individuals) of **trees > 70 cm dbh** in a line survey of 290 ha in the Minkébé area.

Euphorbiaceae (9%), Burseraceae (7%).—Fig. 3. The ten most common species of medium or small size are *Polyalthia suaveolens, Santiria trimera, Cryptosepalum congolanum, Plagiosiphon multijugus, Scorodophloeus zenkeri, Centroplacus glaucinus, Dichostemma glaucescens, Plagiostyles africana, Coula edulis,* and *Cola rostrata.*

From the tree inventory it is clear that some species do not occur as big trees with dbh > 70 cm in the 500 m relevé, but are restricted to the 100 m plots as smaller individuals. One example is *Gilbertiodendron ogoouense.* This species can be considered as understorey species, never reaching great height or diameter. These smaller trees provide a means of subdividing the vegetation types defined by the larger trees.

Various other species may be considered as typical understorey species, such as *Cola rostrata, Coula edulis* and, *Santiria trimera.* Therefore the species composition of the 10 cm diameter plots is not representative of the upper canopy.

Species which occur in all diameter classes such as *Gilbertiodendron dewevrei, Santiria trimera* and, *Cola rostrata* can be considered as primary species.

The diameter disrriburion and sparial distribution of these common species (Fig. 4) illustrate their differences in stature and ecological preferences. The porential stature of the species decreases from *Gilbertiodendron dewevrei* to *Cola rostrata.* Whereas *Gilbertiodendron dewevrei* and *Cola rostrata* are mutually exclusive, *Santiria trimera* is found in association with both species.

Ecological preferences can be discerned in the survey of large diameter trees (Fig. 5). *Pterocarpus soyauxii* and *Cylicodiscus gabunesis* are common species, the latter found in slightly higher densities. *Gilbertiodendron dewevrei* and *Monopetalanthus pellegrinii* have a very well defined distribution and are mutually exclusive. *Dacryodes buettneri* has a rather local disrriburion but can be found in high densities. *Terminalia superba,* a good indicator for late secondary forest, also occurs very locally with high densities.

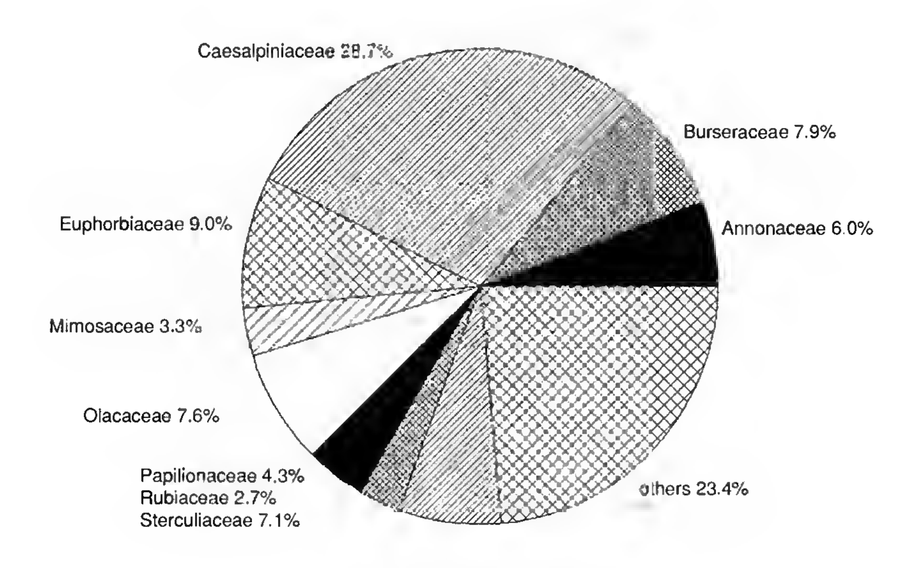


Fig. 3.—Family importance (as percentage of total individuals) of **trees > 10 cm** dbh in a line survey of 3 ha in the Minkébé area.

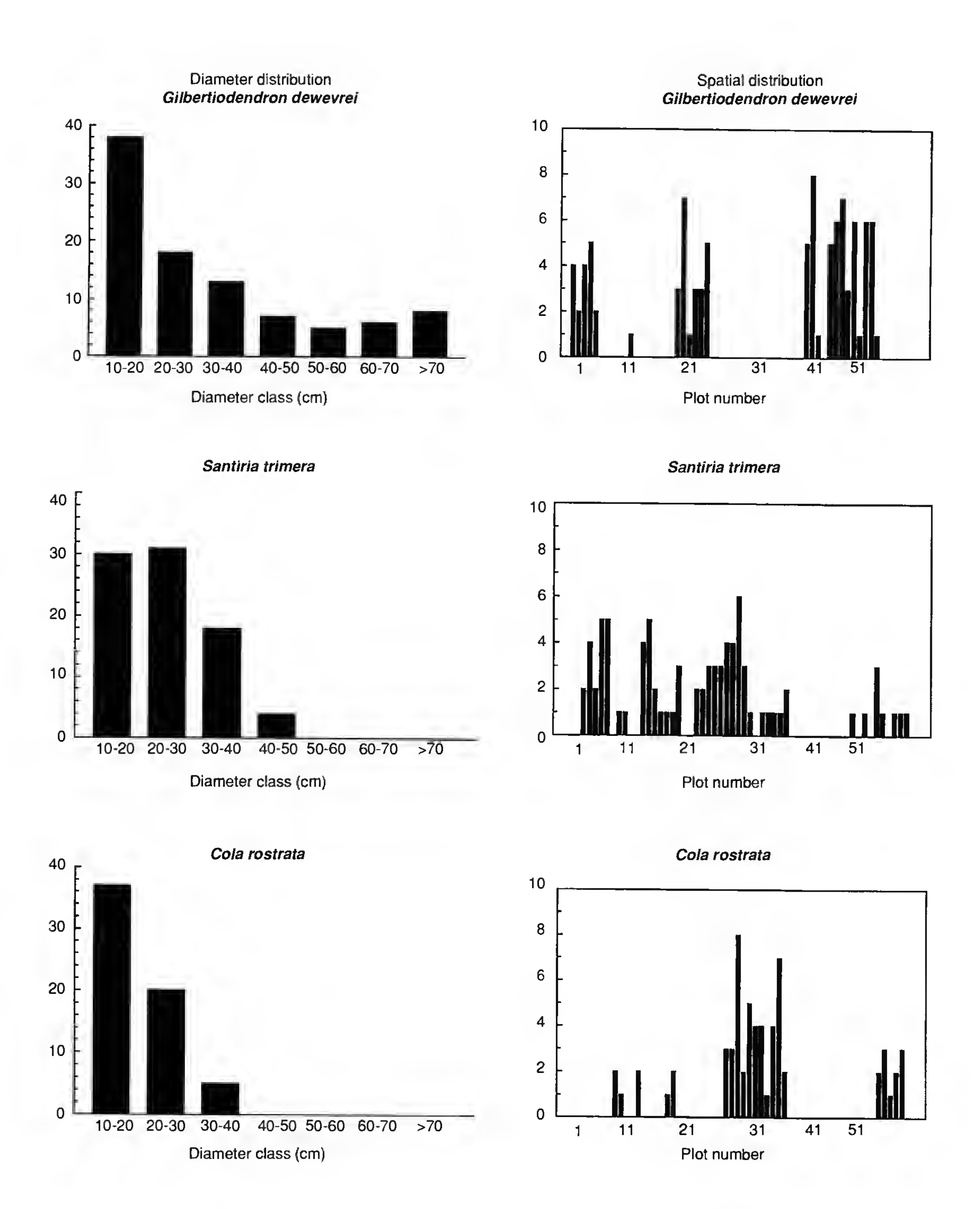


Fig. 4.—Diameter distribution and spatial distribution of three common tree species (per 100 x 5 m plot) along the 6 km transect of trees > 10 cm dbh: *Gilbertiodendron dewevrei*, *Santiria trimera*, and *Cola rostrata*. (*y*-axis: number of trees).

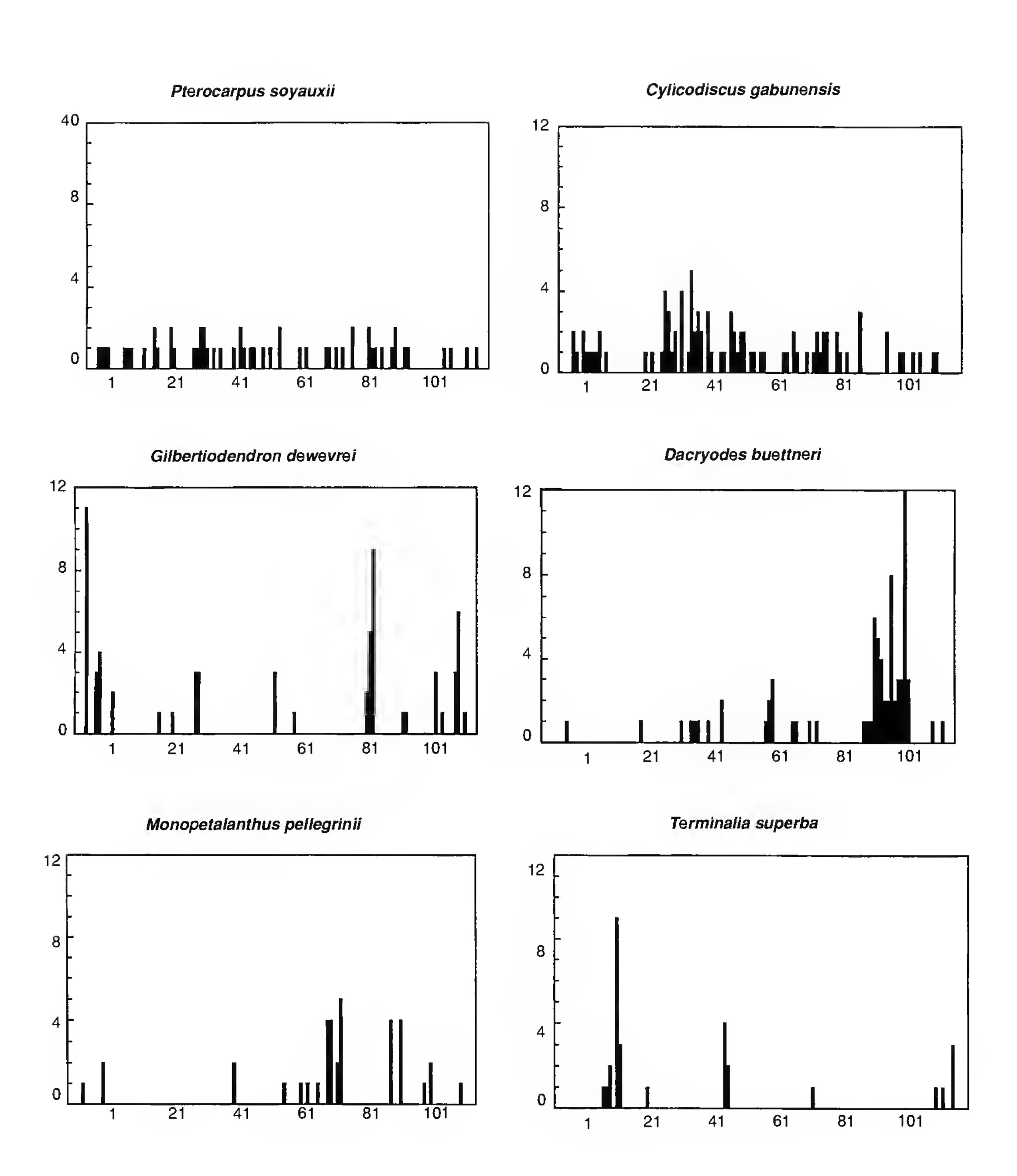


Fig. 5.—Spatial distribution of some characteristic tree species (per 500 × 50 plot) along the 58 km transect of trees > 70 cm dbh: *Pterocarpus soyauxii*, *Cylicodiscus gabunensis*, *Gilbertiodendron dewevrei*, *Dacryodes buettneri*, *Monopetalanthus pellegrinii*, and *Terminalia superba*. (*x*-axis: plot number; *y*-axis: number of trees).

Description of the vegetation types

The name of each vegetation type is based on two species of which one is a more common with highest frequency class, and the second is either a differential or an accompanying species. A differential species is differential for a cluster if its frequency is at least 30% (= one frequency class) higher than in any other cluster, or two related clusters (Schaminée et al. 1995). Occasionally a species was considered differential when it occurred in a frequency of 20% higher than in any other cluster.

When no differential species were present or no clear dominant species the second most important species was taken to name the type.

Typology of the 500 m length plots

In total 115 plots of 500 × 50 m were sampled (one plot was empty). The number of relevés used for clustering is 101 as all the relevés with fewer than 5 individual trees of > 70 cm dbh (n = 14) were not included.

From the ordered Twinspan table five main clusters can be distinguished. These can be described in terms of frequency and relative abundance of the species present and treated as vegetation types. Table 5 presents the synoptic table of the discerned clusters and vegetation types.

Type A: *Gilbertiodendron dewevrei - Pterocarpus soyauxii* type (11 relevés).
This type is very characteristic because of the high frequency of *Gilbertiodendron dewevrei* with high average abundance. In fact *Gilbertiodendron* is the only characteristic species. *Oxystigma buchholzii* occurs in this type only, but with low frequency. In general this type is poor in species (average 5.2). In comparison with all the following types *Cylicodiscus gabunensis* and *Erythrophleum ivorense* are virtually absent.

Type B: *Dacryodes buettneri - Baillonella toxisperma* type (21 relevés).
This type is characterised by the high occurrence of *Dacryodes buettneri* and relatively high presence of *Baillonella toxisperma* (highest frequency class of all types), both differential species. Common species with relatively high frequency are *Cylicodiscus gabonensis, Piptadeniastrum africanum* and *Erythrophleum ivorense*. Some species occur more in this type than the others, such as *Fagara heitzii*, and *Testulea gabonensis*. *Parkia bicolor* occurs slightly more frequently than in A and D.

Type C: *Monopetalanthus pellegrinii - Cylicodiscus gabunensis* type (27 relevés).
This type is less clearly defined than the latter and the following type. *Monopetalanthus pellegrinii* is the differential species of this type and is abundant. *Monopetalanthus letestui* occurs in this type with highest frequency and is slightly differential.

Type D: *Cylicodiscus gabunensis - Pycnanthus angolensis* type (34 relevés).
This type has no differential species, but *Pycnanthus angolensis* as well as *Distemonanthes benthamianus* are almost confined to this type and the next. *Cylicodiscus gabunensis* occurs with high frequency, but *Monopetalanthus* is absent. *Gambeya lacourtiana* and *Uapaca paludosa* are present mainly in this type. Average number of species is higher than in the previous types.

Type E: *Terminalia superba - Ceiba pentandra* type (8 relevés).
This type is characterised by four differential species, three with high frequencies (highest of all types) and relatively high abundance i.e. *Terminalia superba, Alstonia boonei* and *Ceiba pentandra*, and *Celtis adolfi-friderici*. The common species which occur in A, B, C and D are present in this type, but all with low frequency. *Pycnanthus angolensis* is present with higher frequency, but with slightly lower average abundance than in type D. *Blighia welwitschii* and *Mitragyna stipulosa* are confined to this type, and may also be considered as differential.

Typology of the 100 m length plots

In total, 59 plots of 100 × 5 m were sampled (one plot was empty). From the ordered Twinspan table 4 vegetation types could be distinguished, two of which have subtypes. The frequencies of each species in the relevés of each (sub)type are given in Table 6.

Type 1 (cluster 1 + 2): *Gilbertiodendron dewevrei - Gilbertiodendron ogoouense* maintype (22 relevés).
This type is characterised by the high frequency as well as abundance of *Gilbertiodendron dewevrei* and relatively high frequency (40-60%) of *Gilbertiodendron ogoouense*, both differential species for clusters 1 and 2. This type can be divided into two subtypes namely:
1.a: subtype with *Oxystigma buchholzii* and *Cryptosepalum congolanum* (12 relevés).
Oxystigma buchholzii, *Cryptosepalum congolanum*, *Treculia africana*, *Plagiosiphon multijugus* and *Uapaca heudelotii* are differential species for this type, compared with all other types. There are hardly any common species in this subtype.
1.b: subtype with *Santiria trimera* and *Lasiodiscus marmoratus* (10 relevés).
Lasiodiscus marmoratus is differential for this subtype and *Santiria trimera* is frequent, both are absent in the previous one. Typical species are *Heisteria parviflora*, *Strombosia scheffleri*, *Baphia spp.* On average this subtype has a higher number of species than subtype 1.a (13.0 vs. 9.5), but all with low frequencies.

Type 2 (cluster 3): *Calpocalyx dinklagei - Grewia coriacea* type (4 relevés).
This type is based on only four relevés and it is therefore doubtful whether it can be considered as a separate type, although it has five differential species: *Calpocalyx dinklagei*, *Grewia coriacea* as well as *Xylopia quintasii*, *Anthonotha macrophylla* and *A.* cf. *ferruginea*. A large number of species is present only in this type, but all with low frequencies (21-40%). In contrast to the next types the common species *Cola rostrata*, *Petersianthus macrocarpus*, *Plagiostyles africana* and *Strombosia pustulata* do not occur.

Type 3 (cluster 4 + 5): *Cola rostrata - Petersianthus macrocarpus* maintype (21 relevés).
This type is characteristed by its high frequency of *Cola rostrata*. *Scorodophloeus zenkeri* also occurs very frequently, as well as *Strombosia pustulata* and *Petersianthus macrocarpus*. This type can be divided into two subtypes:
3.a: subtype with *Coula edulis* (10 relevés).
In this subtype *Polyalthia suaveolens* and *Coula edulis* are very frequent. *Centroplacus glaucinus* is absent contrary to subtype 3.b.
3.b: subtype with *Strombosia pustulata* (11 relevés).
Strombosia pustulata and *Plagiostyles africana* occur more frequent and abundant in this type than in subtype 3.a. *Dichostemma glaucescens* can locally be abundant (4 plots). In this subtype *Polyalthia suaveolens* and *Coula edulis* are poorly represented in comparison with subtype 3.a.

Type 4 (cluster 6): *Santiria trimera - Centroplacus glaucinus* type (12 relevés).
This type is characterised by the presence of *Centroplacus glaucinus* and *Scorodophloeus zenkeri* with highest frequencies of all types. There are no differential species for this type. *Polyalthia suaveolens* and *Plagiostyles africana* occur also frequently. *Cola rostrata* and *Petersianthus macrocar-*

Capital letters = 500 m plots vegetation types
Numbers = 100 m plots vegetation types
| = bounderies between 500 m plots
¦ = assumed bounderies of the main vegetation types
≈ = creek

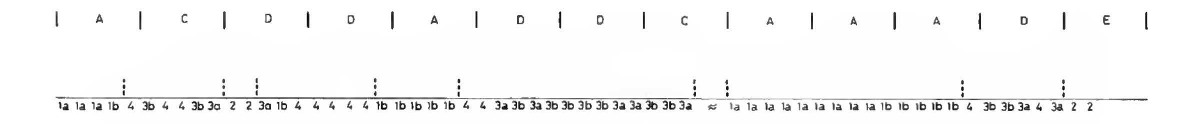


Fig. 6.—A schematic presentation of the occurrence of the 500 m and 100 m vegetation types in the Minkébé survey.

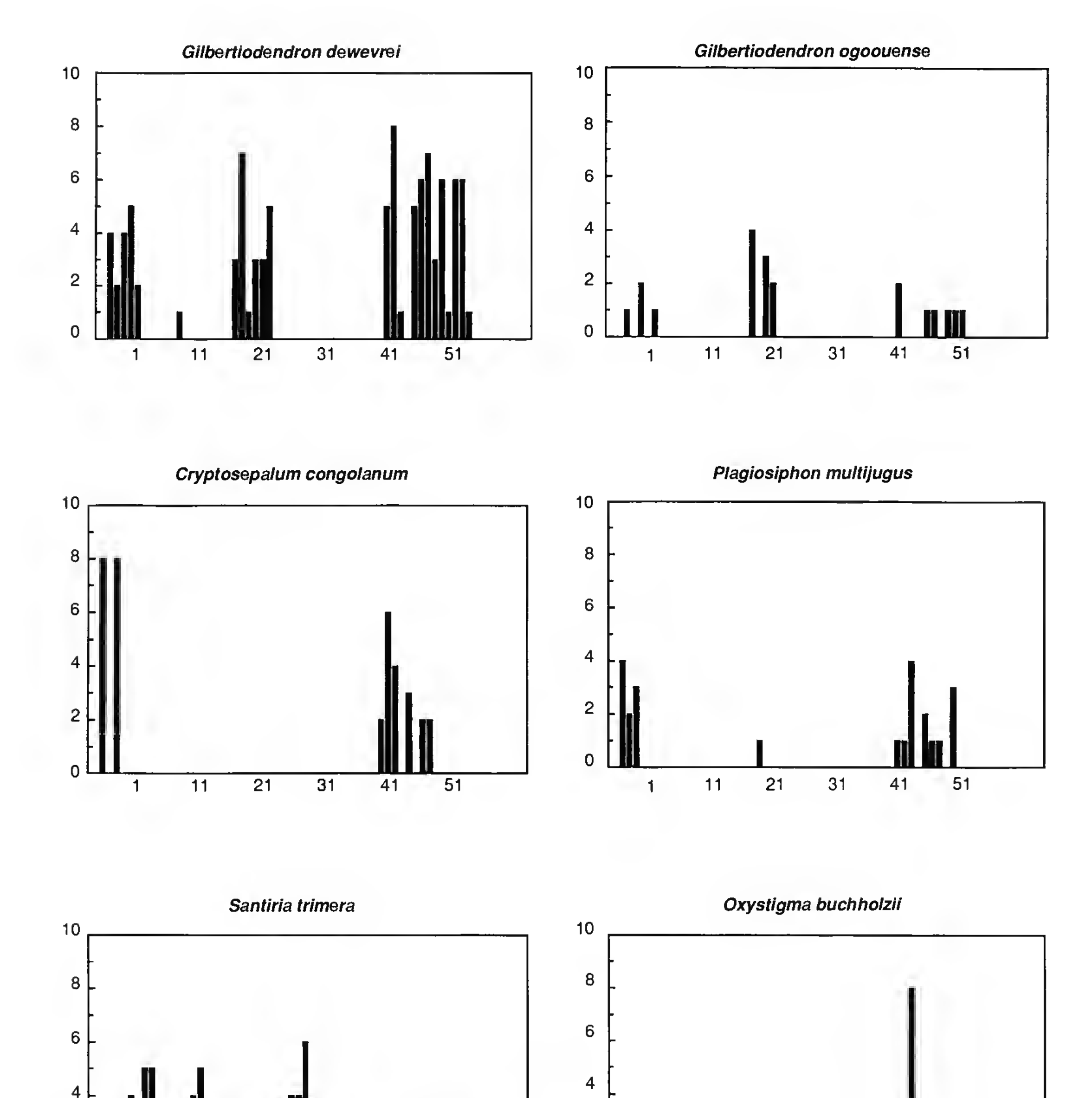


Fig. 7.—Spatial distribution of some characteristic tree species (per 100 × 5 m plot) along the 6 km transect of trees > 10 cm dbh: *Gilbertiodendron dewevrei*, *Gilbertiodendron ogoouense*, *Cryptosepalum congolanum*, *Plagiosiphon multijugus*, *Santiria trimera*, and *Oxystigma buchholzii*. (*x*-axis: plot number; *y*-axis: number of trees).

pus are poorly represented, compared to type 3.a and 3.b, with which type 4 shows great similarity.

Combination of 500 m plots with the 100 m plots

Figure 6 gives in schemaric form the occurrence of the 500 m and 100 m types in the transect. Combining the types derived from the small plots with those from the large plots we see some striking features.

Type 1.a and 1.b coincide with main type A. This type now can clearly be subdivided into a *Gilbertiodendron dewevrei* type with *Oxystigma buchholzii* and a *Gilbertiodendron* type without *Oxistygma*, whereby rhe first type occurs close to rhe streams and the latter on somewhat drier places adjacenr.

The ecological preferences of some smaller species occurring in the two subtypes of the *Gilbertiodendron* maintype are illustrated in Figure 7. *Gilbertiodendron dewevrei* and *G. ogoouense* are found in both wet and dry habitats, *Cryptosepalum congolanum* and *Plagiosiphon multijugus* are only present in the wet habitat and *Oxystigma buchholzii* is confined to the permanently inundated sites along the river. Contrary to this *Santiria trimera* is only present in the drier land habitat.

Type A is clearly primary forest; of the constituting species all diameter classes are represented, forming large almost monospecific patches.

There are no smaller plot types which coincide with type B, but from the large tree inventory alone type B can be classified as primary forest, because of absence of clear secondary species.

Type C and type D are closely related types. The main difference is that D shows more signs of former disturbances through the occurrence, in higher frequencies and/or higher abundance of a number of secondary species, such as e.g. *Pycnanthus angolensis, Distemonanthus benthamianus, Petersianthus macrocarpus*. The abundance of *Cylicodiscus*, one of the main primary species in C and D, is almost equal.

This difference is also reflected in the types 3.a, 3.b as well as type 4, which are also very related to each orher, all three corresponding with types C and D. Types 3.a, 3.b and 4 represent development stages of forest growth from secondary to primary, type 4 having already more primary species with higher abundance than 3.a; while in type 3.a the primary species occur in higher frequency and slightly more abundant than in 3.b.

There are no smaller plot types which coincide with type B, but from the large tree inventory alone type B can be classified as primary forest, because of absence of clear secondary species.

Type 2 of which only 4 relevés are present seems to coincide mainly with E (3 out of 4 relevés) and slightly with D. The large size *Terminalia superba, Ceiba pentandra* and *Eribroma oblongum* indicate that type E may be classified as late secondary forest. The presence of *Anthonotha macrophylla* and *Xylopia quintasii* in the 100 m plots indicates that the forest is changing into primary forest.

As there probably are more changes taking place in the composition of smaller trees than in the large trees it is difficult to show very strict correlations between the types of the 100 m plots and the 500 m plots.

DISCUSSION

The data on family and species importance of trees > 70 cm dbh can be compared with the data of CABALLÉ (1978) concerning trees > 60 cm dbh (see Table 1 + Table 2).

Comparing the data on family importance of large trees from CABALLÉ (1978) with the Minkébé results, the importance of Caesalpiniaceae is (almost) the same, Mimosaceae are more important in the Minkébé survey, but Myristicaceae importance is much lower (Table 1). If we compare the importance of the tree species (Table 2), the absence of *Scyphocephalum ochocoa* in the Minkébé survey is noticeable and this explains also the low importance value of Myristicaceae. The higher value for *Piptadeniastrum africanum* and *Cylicodiscus gabunensis* in Minkébé accounts for the higher importance value of Mimosaceae. Though the relative frequency of Caesalpiniaceae is the same, the share of the constituting species differs. *Gilletiodendron pierreanum* is absent in the Minkébé survey, and *Distemonanthus benthamia-*

TABLE 1.—Comparison of family importance of large trees in the Minkébé area (290 ha) with the results of CABALLÉ (1978) for East Gabon. Values in % of total number of trees.

	CABALLÉ * dbh > 60 cm**	Minkébé dbh > 70 cm
Caesalpiniaceae	26.7	27.1
Burseraceae	4.2	7.0
Irvingiaceae	2.6	3.5
Olacaceae	2.4	
Mimosaceae	14.6	20.9
Papilionaceae	3.1	5.3
Myristicaceae	8.5	3.9

* : Based on the 15 most abundant species.
**: Based on all individuals of all species present.

nus, *Erythrophleum ivorense* and *Monopetalanthus pellegrinii* are not among the 15 most important species of CABALLÉ (1978).

The data on family and species importance of trees > 10 cm dbh can be compared with the data of CABALLÉ (1978) concerning trees 20 cm < dbh < 60 cm (see Table 3 + Table 4).

The family importance value of small and medium sized trees (Table 3) shows an extremely high value for Caesalpiniaceae in the Minkébé survey (when compared to CABALLÉ). This is caused by the fact that 23 of the 59 relevés (39%) are located in *Gilbertiodendron* forest, whereas in the survey of trees > 70 cm dbh only 11 of the 104 relevés (11%) are located in *Gilbertiodendron* forest. Comparing the relative frequency values of CABALLÉ (1978) with the Minkébé data, the difference in importance value of Caesalpiniaceae is illustrated with the higher value of *Gilbertiodendron spp.* and the 5 additional Caesalpiniaceae species in Minkébé (Table 4).

The data of the survey of trees > 10 cm dbh can also be compared with the results of REITSMA at Ekobakoba (REITSMA 1988), which is most proximate to the Minkébé area. REITSMA's one-hectare plot, on the top of a small hill with little variation in relief, comprised 438 individuals > 10 cm dbh, 85 species in 30 families. The three most important families are also Caesalpiniaceae, Euphorbiaceae and Burseraceae.

According to REITSMA (1988, table 9, page 46), who uses importance values, the ten most important species are *Hymenostegia pellegrinii*, *Scyphocephalum ochocoa*, *Santiria trimera*, *Dialium pachyphyllum*, *Plagiostyles africana*, *Desbordesia glaucescens*, *Dacryodes buettneri*, *Cola rostrata*, *Polyalthia suaveolens*, and *Entandrophragma candollei* (a single tree only).

The average density of trees > 10 cm dbh in the Minkébé area is 385 trees per ha, which is less than in REITSMA's Ekobakoba site, who found 438 individuals in one hectare. This can be attributed to the fact that part of the survey was situated in the dynamic river system of the river Sing. The higher number of species found cannot only be attributed to the larger area surveyed, but is surely also caused by the greater environmental diversity, since swamps, periodically flooded forest and dry forest are included in the survey.

The high value for *Hymenostegia pellegrinii* in the Ekobakoba plot and its absence in the Minkébé survey of trees > 10 cm is another example of local dominance of certain Caesalpiniaceae species. The high value is also caused by the small sample size/area surveyed. REITSMA's plot is a 100 × 100 m plot with little

TABLE 2.—Comparison of species importance of large trees for the 15 highest ranking species in the Minkébé area (290 ha) with the results of CABALLÉ (1978) for East Gabon. Values in % of total number of trees.

	CABALLÉ dbh > 60 cm	Minkébé dbh > 70 cm
Scyphocephalum ochocoa	5.2	
Pentaclethra eetveldeana	4.5	3.7
Gilletiodendron pierreanum	4.2	
Pycnanthus angolensis	3.3	3.7
Petersianthus macrocarpus	3.1	2.7
Alstonia boonei	3.0	2.6
Dacryodes buettneri	2.9	6.5
Piptadeniastrum africanum	2.9	4.2
Cylicodiscus gabunensis	2.6	7.9
Celtis brieyi	2.5	
Gilbertiodendron sp.	2.4	5.6
Pterocarpus soyauxii	2.3	4.8
Uapaca sp.	2.3	1.1
Scorodophloeus zenkeri	2.0	1.1
Terminalia superba	2.0	2.5
Distemonanthus benthamianus		3.5
Erythrophleum ivorense		5.3
Monopetalanthus pellegrinii		2.3

TABLE 3.—Comparison of family importance of small and medium sized trees in the Minkébé area (3 ha) with the results of CABALLÉ (1978) for East Gabon. Values in % of total number of trees.

	CABALLÉ * 20 cm < dbh < 60 cm	Minkébé ** dbh > 10 cm
Euphorbiaceae	8.1	9.0
Caesalpiniaceae	9.3	28.7
Burseraceae	6.9	7.9
Mimosaceae	5.0	3.3
Annonaceae	3.3	6.0
Lecythidaceae	3.1	
Ulmaceae	2.3	
Olacaceae	2.0	7.6
Myristicaceae	2.8	
Pandaceae	1.2	

* : Based on the 15 most abundant species.
**: Based on all individuals of all species present.

variation in relief. The Minkébé survey is a three ha plot of 6000 × 5 m with much more variation in topography and abiotic factors. The chances for local dominance over the entire plot are much smaller. CABALLÉ's surface area covers vast stretches of the eastern zone of Gabon and therefore high species importance values are impossible.

When comparing family importance values of trees > 60 cm dbh with 20 cm < trees < 60 cm of CABALLÉ (1978) it is clear that Caesalpiniaceae and Mimosaceae are very important canopy trees (41.3%) but are far less prominent (14.4%) among small and medium sized trees (the floristic composition of small and medium sized trees is more diverse).

The recognized vegetation types of the 500 m as well as 100 m plots show the internal dyna-

TABLE 4.—Comparison of species importance of small and medium sized trees for the 15 highest ranking species in the Minkébé area (3 ha) with the results of CABALLÉ (1978) for East Gabon and REITSMA (1988) at Ekobakoba (1 ha). Values in % of total number of trees.

	REITSMA * dbh > 10 cm	Minkébé dbh > 10 cm	CABALLÉ 20 cm < dbh < 60 cm
Plagiostyles africana	5.3	1.8	8.1
Scorodophloeus zenkeri		5.0	6.4
Santiria trimera	5.3	7.2	5.8
Pentaclethra eetveldeana		1.4	3.9
Polyalthia suaveolens	3.3	2.9	3.2
Petersianthus macrocarpus		1.6	3.1
Celtis brieyi			2.3
Coula edulis		3.5	2.0
Scyphocephalum ochocoa	3.3		1.4
Dialium pachyphyllum	4.6		1.7
Coelocaryon preusii			1.4
Gilbertiodendron dewevrei		8.2	1.3
Gilbertiodendron ogoouense		1.7	
Panda oleosa			1.2
Pentaclethra macrophylla			1.1
Dacryodes buettneri	2.0		1.1
Desbordesia glaucescens	2.5		
Entandrophragma candollei	0.3		
Hymenostegia pellegrinii	7.6		
Cola rostrata	4.6	5.4	
Centroplacus glaucinus		1.9	
Cryptosepalum congolanum		3.0	
Dichostemma glaucescens		2.3	
Oxystigma buchholzii		1.6	
Plagiosiphon multijugus		2.0	

*: 10 most important species according to REITSMA's importance value.

TABLE 5.—Synoptic table of the vegetation types of the 500 m plots (trees dbh > 70 cm) of the Minkébé area (for codes see below).

Cluster	1	2	3	4	5
Vegetation type	A	B	C	D	E
Number of relevés	11	21	27	34	8
Aver. no. of species	5.2	7.9	7.8	9.0	7.9
Standard deviation	2.7	3.2	2.4	2.9	3.3
Differential species					
Gilbertiodendron dewevrei	V	I	+	I	-
Oxystigma buchholzii	II	-	-	-	-
Baillonella toxisperma	I	III	+	I	-
Monopetalanthus letestui	I	I	II	-	-
Monopetalanthus pellegrinii	-	I	III	-	-
Dacryodes buettneri	II	IV	II	II	-
Alstonia boonei	I	I	I	II	IV
Pycnanthus angolensis	-	I	-	III	IV
Terminalia superba	-	-	I	I	IV
Distemonanthus benthamianus	-	-	I	III	IV
Gambeya lacourtiana	-	-	-	II	I
Celtis adolfi-friderici	-	-	-	I	II
Xylopia hypolampra	-	-	+	I	II
Ceiba pentandra	-	-	-	-	III
Blighia welwitschii	-	-	-	+	II
Mitragyna stipulosa	-	-	-	-	II
Common species					
Petersianthus macrocarpus	-	I	I	II	II
Pentaclethra eetveldeana	I	II	I	II	III
Pterocarpus soyauxii	III	I	III	III	I
Erythrophleum ivorensis	I	III	III	III	II
Cylicodiscus gabunensis	I	III	IV	III	-
Hymenostegia pellegrinii	II	I	I	I	-
Piptadeniastrum africanum	II	III	III	II	-
Irvingia grandifolia	I	-	I	I	II
Guibourtia tessmannii	I	I	-	I	-
Parkia bicolor	I	II	-	I	-
Fagara heitzii	-	II	I	I	-
Scorodophloeus zenkeri	I	I	+	I	-
Millettia laurentii	-	+	I	-	II
Klainedoxa gabonensis	-	I	I	I	I
Pentaclethra macrophylla	-	I	II	II	-
Celtis tessmannii	-	I	I	II	-
Other species (excluding rare)					
Amphimas pterocarpoides	-	-	+	I	I
Beilschmiedia sp.	-	-	I	+	I
Uapaca paludosa	-	I	-	II	-
Detarium macrocarpum	I	-	I	I	-
Anopyxis klaineana	-	+	I	I	I
Celtis mildbraedii	I	-	+	I	I
Canarium schweinfurtii	-	+	+	I	-
Coula edulis	-	I	I	-	-
Dialium pachyphyllum	-	I	I	-	-
Dialium dinklagei	-	I	+	+	-
Erismadelphus exsul	-	I	I	I	-
Fillaeopsis discophora	-	I	I	I	-
Entandrophragma cylindricum	I	-	+	I	-
Entandrophragma candollei	-	+	I	I	-
Parkia filicoidea	-	+	I	+	-
Irvingia gabonensis	-	-	+	I	I

Milicia excelsa	-	-	+	+	I
Lophira alata	I	-	-	-	I
Syzygium sp.	-	I	-	I	I
Dracaena mannii	-	+	-	I	I
Nauclea diderichii	-	+	I	I	-
Pterygota bequaertii	I	-	-	I	-
Tessmannia africana	I	+	-	+	-
Tessmannia anomala	I	-	I	-	-
Tetraberlinia bifoliolata	I	-	+	I	-
Turraeanthus africanus	I	-	-	I	-

Rare species

Afzelia bipindensis: D,+; *Albizia adianthifolia*: B,+; D,I; *Albizia ferruginea*: D,I; *Antiaris africana*: B,+; *Antrocaryon micraster*: B,I; C,+; *Bombax bunoponense*: A,I; D,I; *Coelocaryon preussii*: D,+; *Crudia gabonensis*: B,+; D,+; *Dacryodes igaganga*: C,+; *Daniellia oblongum*: C,+; *Desbordesia glaucescens*: B,I; *Diogia zenkeri*: C,+; *Drypetes gosweilleri*: C,+; *Entandrophragma congoense*: C,I; *Eribroma oblongum*: C,+; D,I, *Ficus elasticoides*: D,+; *Gambeya beguei*: C,+; D,+; *Guarea thomsonii*: D,I; *Gilbertiodendron ogoouense*: B,+; *Heisteria parvifolia*: E,I; *Julbernardia seretii*: C,+; *Kayodendron bridelioides*; D,+; *Klainedoxa trillesii*: C,+; D,I; *Landolphia foretii*: C,+; *Lovoa trichilioides*: A,I; B,I; *Macaranga* sp.: A,I; *Mammea africana*: A,I; *Maranthes glabra*: B,I; *Maranthes* sp.: B,+; C,+; *Myrianthus arboreus*: E,I; *Newtonia glandulifera*: C,+; *Newtonia* cf. *glandulifera*: B,+; *Oldfieldia africana*: B,+; C,I; *Ongokea gore*. B,I; C,I; *Parinari excelsa*: B,+; C,+; *Pachyelasma tessmannii*: B,+; *Panda oleosa*: C,+; D,I; *Pteleopsis hylodendron*: C,+; D,I; *Pterygopodium oxyphyllum*: B,I; D,+; *Rhodognaphalon brevicuspe*: C,+; *Scottellia klainei*: D,I; *Staudtia gabonensis*: D,I; *Stemenocoleus micranthus*: B,I; *Strombosia scheffleri*: C,+; *Testulea gabonensis*: B,I; C,+; *Tieghemella africana*: B,+; *Trichilia tessmannii*. C,I, *Trichoscypha acuminata*: B,+; *Tridesmostemon omphalocarpoides*: C,+; *Uapaca heudelotii*: B,+.

Frequencies in 5 classes

-	= species not present in the relevés of the cluster
+	= species present in 1-5% of the relevés
I	= species present in 6-20% of the relevés
II	= species present in 21-40% of the relevés
III	= species present in 41-60% of the relevés
IV	= species present in 61-80% of the relevés
V	= species present in 81-100% of the relevés

mics of the forest, with young and old stages alternating over short and long distances (Fig. 6). As the inventory took place along a transect with adjacent plots it could be expected that the typology would be less pronounced. Figure 6 shows the borders between each sample plot. On the basis of the typology the assumed boundaries between the different vegetation types are drawn.

More data are needed before something can be said about the successional status of the different types (Type D either a transitory type having elements of Type A or transitory to E, having various species in common with E). It also contains fewer individuals and fewer species in comparison with the other types. It is either not yet completely developed to mature forest or in a degraded phase.

As little was recorded about the soil and the local topography, not much can be said about the ecology of the vegetation types, except for the *Gilbertiodendron dewevrei* - *Oxystigma* subtype, which occurs primarily along streams and is inundated. Medium size trees are *Oxystima buchholzii* and *Plagiosiphon multijugus*. The *Gilbertiodendron dewevrei* - *Santiria trimera* forest, on drier places, has a canopy dominated by *Gilbertiodendron dewevrei*, but *Oxystigma* is absent, while medium trees include *Santiria trimera*, *Strombosia scheffleri*, *Coula edulis* and *Carapa procera*.

The vegetation types described in this study are but local types of which the syntaxonomic significance can only be determined if far more relevés from nearby regions become available. Ecological parameters such as soil characteristics, hydrology, local topography and human influen-

TABLE 6.—Synoptic table of the vegetation types of the 100 m plots (trees > 10 cm) of the Minkébé area (for codes see below).

Cluster	1	2	3	4	5	6
Vegetation type	1a	1b	2	3a	3b	4
Number of relevés	12	10	4	10	11	12
Aver. no. of species	9.5	13.1	12.8	14.0	12.5	13.8
Standard deviation	3.1	2.4	3.2	4.0	1.3	2.8
Differential species						
Cryptosepalum congolanum	IV	-	-	-	-	-
Oxystigma buchholzii	IV	-	-	-	-	-
Uapaca heudelotii	II	-	-	-	-	-
Treculia africana	III	-	-	-	-	-
Plagiosiphon multijugus	IV	I	-	-	-	-
Lasiodiscus marmoratus	-	II	-	-	-	-
Gilbertiodendron ogoouensis	III	III	-	-	I	-
Gilbertiodendron dewevrei	V	V	II	-	-	II
Anthonotha cf. *ferruginea*	-	-	III	-	-	-
Anthonotha macrophylla	I	-	III	I	-	-
Xylopia quintasii	-	-	IV	II	-	-
Calpocalyx dinklagii	-	II	IV	II	I	I
Grewia coriacea	-	-	IV	I	I	II
Cola rostrata	-	-	-	IV	V	II
Petersianthus macrocarpus	-	-	-	III	IV	I
Trichoscypha acuminata	-	-	-	-	II	I
Common species						
Santiria trimera	-	III	II	V	IV	V
Coula edulis	-	II	II	IV	II	IV
Polyalthea suaveolens	-	I	II	III	I	IV
Pentaclethra eetveldeana	-	I	II	II	I	III
Dialium pachyphyllum	II	II	-	I	II	I
Beilschmiedia sp.	I	II	II	II	I	-
Scorodophloeus zenkeri	-	-	II	IV	IV	V
Plagiostyles africana	-	II	-	I	IV	III
Centroplacus glaucinus	-	-	II	-	III	IV
Strombosia pustulata	-	I	-	III	V	III
Celtis tessmannii	-	I	-	II	I	I
Pausinystalia macroceras	-	I	II	-	III	II
Dichostemma glaucescens	I	I	-	-	II	I
Panda oleosa	I	I	III	-	-	III
Sorindeia nitidula	-	I	-	-	I	II
Trichilia welwitschii	-	-	II	I	I	-
Picralima nitida	-	-	II	I	I	-
Irvingia gabonensis	I	I	-	I	I	-
Indet.	II	II	III	I	II	II
Other species (excluding rare)						
Strombosia scheffleri	-	II	-	I	-	I
Heisteria parvifolia	-	II	-	I	-	I
Baphia buettneri	-	II	-	I	-	I
Mareyopsis longifolia	-	I	II	II	-	-
Carapa procera	-	I	-	I	I	I
Tetraberlinia bifoliata	-	I	-	I	-	II
Baphia pubescens	-	-	II	I	-	I
Pterocarpus soyauxii	-	I	II	-	-	I
Dacryodes klaineana	-	I	-	I	-	I
Dialium dinklagei	-	I	-	-	I	I
Afrostyrax lepidophyllus	-	-	-	II	II	I
Drypetes gossweileri	-	-	-	I	I	I
Garcinia gnetoides	-	I	-	I	-	I

Staudtia gabonensis	-	I	-	-	I	I
Xylopia parviflora	-	I	-	I	-	I
Pseudospondias sp.	-	I	II	-	-	-
Pachypodanthium staudtii	-	-	II	-	-	I
Markhamia tomentosa	-	-	II	-	I	-
Xylopia hypolampra	-	-	II	I	-	-
Alstonia boonei	-	-	II	I	-	-
Rauvolfia caffra	I	-	II	-	-	-
Sapium cornutum	-	-	II	-	-	I
Irvingia grandifolia	-	-	II	-	-	I
Ochthocosmus sp.	-	-	II	I	-	-
Psychotria sp.	I	-	II	-	-	-
Erythrophleum ivorensis	-	-	-	-	II	-
Pycnanthus angolensis	-	-	II	-	-	-
Terminalia superba	-	-	II	-	-	-
Diospyros piscatoria	-	-	II	-	-	-
Maesopsis eminii	-	-	II	-	-	-
Nauclea diderichii	-	-	II	-	-	-
Rothmannia whitfieldii	-	-	II	-	-	-
Tricalysia biafrana	-	-	II	I	-	-
Grewia sp.	-	-	II	-	-	-
Celtis mildbraedii	-	-	II	-	-	-

Rare species

Albizia adianthifolia: 4,I; *Albizia ferruginea*: 4,I; *Angylocalyx sp.*: 1b,I; 3b,I; *Annonidium mannii*: 3b,I; 4,I; *Anopyxis klaineana*: 4,I; *Aphanocalyx cynometroides*: 1b,I; *Artabotrys sp.*: 3a,I; *Baikiea insignis*: 1b,I; *Baphia* cf. *leptostemma*: 1b,I; *Baphia sp.*: 1b,I; *Baphia sp.*: 1b,I; *Baphia sp.*: 3a,I; *Baphia sp.*: 1b,I; 3b,I; *Baphia sp.*: 1b,I; 3a,I; *Berlinia sp.*: 1b,I; *Blighia sp.*: 3a,I; *Bridelia micrantha*: 1b,I; *Caloncoba welwitschii*: 3a,I; *Camptostylis mannii*: 1a,I; 3a,I; *Celtis adolfi-friderici*: 1b,I; *Chytranthus sp.*: 3b,I; *Clerodendron sp.*: 4,I; *Coelocaryon preussi*: 3a,I, *Coffea sp.*: 1a,I; *Cola verticillata*: 1b,I; *Cola sp.*: 1b,I; *Cola sp.*: 1b,I; *Cola sp.*: 1b,I; 3a,I; *Cola sp.*: 4,I; *Cola sp.*: 3a,I; *Combretum homalioides*: 4,I; *Combretum sordidum*: 3a,I; 3b,I; *Combretum sp.*: 4,I; *Cylicodiscus gabunensis*: 3a,I; 4,I; *Cynometra sanagaensis*: 1a,I; *Dacryodes buettneri*: 4,I; *Dalbergia sp.*: 1a,I; 1b,I; *Dalhousiea africana*: 3b,I; *Detarium macrocarpum*: 1b,I; 4,I; *Dichapetalum choristilum*: 3b,I; *Didimosalpinx abbeokutae*: 1b,I; *Diospyros ferrea*: 1a,I; *Diospyros gilletii*: 1a,I; *Diospyros mannii*: 1b,I; 3a,I; *Discoglypremna caloneura*: 1b,I; *Distemonanthus benthamianus*: 3a,I; 3b,I; *Drypetes sp.*: 3b,I; 4,I; *Entandrophragma cylindricum*: 4,I; *Eribroma oblonga*; 3b,I; *Eriocoelon sp.*: 3a,I; *Gambeya boukokoensis*: 4,I; *Gambeya lacourtiana*: 3a,I; 3b,I; *Garcinia mannii*: 4,I; *Garcinia staudtii*: 3a,I; *Gardenia imperialis*: 1a,I; *Grewia pinnatifida*: 1a,I; 1b,I; *Grewia sp.*: 3a,I; *Griffonia sp.*: 4,I; *Guarea cedrata*: 3a,I; *Klainedoxa gabonensis*: 3a,I; *Landolphia foretii*: 3b,I; *Lindackeria dentata*: 3a,I; 4,I; *Lonchocarpus sp.*: 1a,I; *Lophira alata*: 1b,I; *Macaranga sp.*: 1a,I; *Magnistipula zenkeri*: 1a,I; *Mallotus oppositifolius*: 1a,I; *Mammea africana*: 1a,I; 3a,I; *Maprounea africana*: 1b,I; *Massularia acuminata*: 3a,I; *Microdesmis sp.*: 1a,I; *Milicia excelsa*: 3b,I; *Millettia bipindensis*: 1b,I; *Millettia laurentii*: 1b,I; 3b,I; *Millettia sp.*: 1a,I; *Monopetalanthus microphyllus*: 3b,I; 4,I; *Napoleonaea sp.*: 1a,I; *Nauclea pobeguinii*: 1a,I; *Nauclea vanderguchtii*: 1a,I; *Neuropeltis acuminata*: 1b,I; *Octolobus heteromerus*: 3a,I; *Odyenda gabonensis*: 3b,I; 4,I; *Omphalocarpum procerum*: 3b,I; *Oubanguia* cf. *africana*: 1a,I; 1b,I; *Pachypodanthium confine*: 4,I; *Pancovia sp.*: 3a,I; 4,I; *Parinari excelsa*: 1b,I; *Pausinystalia johimbe*: 3b,I; 4,I; *Piptostigma glabrescens*: 1b,I; *Plagiosiphon emarginatus*: 1a,I; *Porterandia cladantha*: 3a,I; *Pterocarpus sp.*: 1a,I; *Pterygota bequaertii*: 4,I; *Rhaphiostylis sp.*: 3a,I; *Rauvolfia letouzeyi*: 3b,I; *Rinorea kamerunensis*: 3b,I; *Rinorea subsessilis*: 3b,I; *Rinorea welwitschii*: 1b,I; *Sorindeia sp.*: 1b,I; *Sorindeia sparanoi*: 1a,I; *Strephonema mannii*: 1b,I; *Strychnos campicola*: 1a,I; *Synsepalum longecuneatum*: 1b,I; 4,I; *Syzygium sp.*: 4,I; *Tabernaemontana crassa*: 3b,I; *Tessmannia anomala*: 1a,I; *Testulea gabonensis*: 4,I; *Thomandersia laurifolia*: 4,I; *Trichilia monadelpha*: 1a,I, *Trichoscypha sp.*: 3a,I; *Xylopia aethiopica*: 4,I; *Xylopia letestui*: 1b,I; 3a,I; *Xylopia pinaertii*: 3a,I; *Xylopia sp.*: 4,I; *Xylopia staudtii*: 3b,I.

Frequencies in 5 classes

-	= species not present in the relevés of the cluster
+	= species present in 1-5% of the relevés
I	= species present in 6-20% of the relevés
II	= species present in 21-40% of the relevés
III	= species present in 41-60% of the relevés
IV	= species present in 61-80% of the relevés
V	= species present in 81-100% of the relevés

ce are lacking. These will be necessary to confirm the existence of such types and make it possible to interpret the forest types in an ecological sense. Doing so the types can possibly be used for much wider areas. Through species composition these types can only be distinguished as primary or secondary types.

Although not a classical way of making vegetation relevés and typology, whereby for each species in a homogenous sample plot a cover/abundance code is given (KENT & COKER 1992), recording presence/absence plus relative abundance according to the number of individual trees in adjacent plots along a transect, has proved by this study to be a suitable method for defining local forest types (communities). Enumerating cover/abundance of all species of a homogeneous sample plot in rain forest is very time consuming. It should be noted that the present study was initially not meant for making a vegetation classification but a general forest inventory.

The number of 100 m plots (59) may be considered too small to include the great diversity of the forest. More plots are needed and would surely result in clearer differentiation between the recognized types and may reveal additional types. The size of the 100 m plots (100 × 5 m) might be questioned. For relevés in rain forest, enumerating only trees above a certain dbh larger plots are often used. It is beyond the scope of this study to debate the issue of sample plot size and minimum area. The reader is referred to amongst others, HOMMEL (1987, 1990), DE ROUW (1991) and DUIVENVOORDEN & LIPS (1995).

The forest types as distinguished in this survey show that within the general forest classification of CABALLÉ (1978) for eastern Gabon, various associations can occur. CABALLÉ recognized 2 types: a "forêt dense humide sempervirente" with *Scyphocephalum ochocoa*, *Pycnanthus angolensis*, *Pentaclethra eetveldeana*, *Celtis spp.*, *Gilletiodendron pierreanum*, and *Gilbertiodendron dewevrei*; a "forêt dense à tendance semi-caducifoliée" with *Pycnanthus angolensis*, *Pentaclethra eetveldeana*, *Terminalia superba* and *Triplochiton scleroxylon*. These correspond more or less with Types B and E found in the Minkebé area. However, in the Minkébé survey *Scyphocephalum ochocoa*, *Gilletiodendron pierreanum* and *Triplochiton scleroxylon* were not found.

GÉRARD (1960) regarded the *Gilbertiodendron dewevrei* forest in the Uele region (Congo) as a climax vegetation, since it was a self regenerating stable population of this species. ÉVRARD (1968) regarded single dominant forest as the climax type since the dominants, besides being able to regenerate in their own shade, can also invade mixed moist semi-evergreen rain forest, which is usually deficient in regeneration of its own upper canopy species. This contrasts with the opinion of LETOUZEY (1983) who regards the *Gilbertiodendron dewevrei* forests as relicts of a formerly more extensive *Gilbertiodendron* forest, that are steadily being invaded by the surrounding mixed forest species, due to natural or human causes. ÉVRARD and LETOUZEY agree that possibly recent climatic change has been too rapid to allow the *Gilbertiodendron dewevrei* forest to achieve its maximum potential range during those climatic phases of the Pleistocene most favourable for its expansion. The present study reveals that GÉRARD's view on the *Gilbertiondron* forest also applies to the Minkébé region.

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APPENDIX: NEW RECORDS FOR NORTH EAST GABON

Based on MINKÉBÉ collections present at Herbarium Vadense (WAG) and fully documented there. Complete species list (based on VAN VALKENBURG 1990) published as appendix 2b in STEEL (1992). Additional collections from december 1990 have been included for the present list.

Acanthaceae
Justicia tenella (Nees) T. Anderson: W 508
Phaulopsis poggei (Lindau) Lindau: W 427
Rhinacanthus virens (Nees) Milne-Redh.: AM 7; W 153
Alismataceae
Ranalisma humile (Kunth) Hutch.: W 144; Wieringa 614
Anacardiaceae
Sorindeia sparanoi De Wild.: E 32
Annonaceae
Monanthotaxis klainei Pierre ex Engl. & Diels var. *lastoursvillensis* (Pellegr.) Verdc.: AM 26

Pachypodanthium confine Engl. & Diels: C 324, 455; W 65
Uvaria versicolor Pierre ex Engl. & Diels: AM 46
Xylopia parviflora (A. Rich.) Benth.: C 364, 716
Xylopia pynaertii De Wild.: C 789; E 288
Apocynaceae
Baissea baillonii Hua: R 141
Landolphia foretii Jum.: C 112
Rauvolfia caffra Sond.: E 26, 347
Rauvolfia letouzeyi Leeuwenb.: E 270
Tabernaemontana eglandulosa Stapf: W 509
Begoniaceae
Begonia mildbraedii Gilg: W 200, 436
Begonia scutifolia Hook. f.: W 221
Begonia sessilifolia Hook. f.: W 278
Begonia subscutata De Wild.: AM 77; W 171, 361; Wieringa 539, 581
Bombacaceae
Rhodognaphalon brevicuspe (Sprague) Roberty: A 721
Caesalpiniaceae
Amphimas pterocarpoides Harms: A 72, 467
Anthonotha cf. *ferruginea* (Harms) J. Léonard: C 207
Baphiopsis parviflora Benth. ex Baker: W 57; X 237; Y 6, 13
Cynometra sanagaensis Aubrév.: AM 73; E 87; Wieringa 542
Cynometra schlechteri Harms: W 496
Daniellia oblonga Oliv.: A 102
Erythrophleum suaveolens (Guill. & Perr.) Brenan: C 686; S 195
Gilbertiodendron ogoouense (Pellegr.) J. Léonard: AM 72; C 33, 68, 89, 118, 283, 367, 371, 387, 484, 492; E 18; V 1, 140, 180, 231
Guibourtia tessmannii (Harms) J. Léonard: A 77
Julbernardia seretii (De Wild.) Troupin: B 83
Monopetalanthus evrardii P. Bamps: A 50; B 43; C 27, 87, 279, 286; E 16, 69, 139, 167, 182; S 41; W 438
Monopetalanthus letestui Pellegr.: A 360, 609
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Explanation of prefixes in Minkébé collection: A, B: voucher specimen transect trees > 70 cm dbh; C, E: voucher specimen transect trees > 10 cm dbh; R, S, V, X, Y, Z: voucher specimens subplots; AM: André Moungazi; D: Dibata; F: Mondjo, Obiang; W: Wilks.

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Sylvichadsia, a new genus of Leguminosae-Papilionoideae-Millettieae endemic to Madagascar

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ABSTRACT

Sylvichadsia, a new genus in the tribe Millettieae (Leguminosae-Papilionoideae) is described. It includes four species, all endemic to Madagascar (*S. macrophylla* (R. Vig.) Du Puy & Labat, *S. grandifolia* (R. Vig.) Du Puy & Labat, *S. grandidieri* (Baill.) Du Puy & Labat, and *S. perrieri* (R. Vig.) Du Puy & Labat).

MOTS CLÉS
Leguminosae,
Papilionoideae,
Sylvichadsia,
Madagascar.

RÉSUMÉ

Sylvichadsia, un nouveau genre, de la tribu des Millettieae (Leguminosae-Papilionoideae) est décrit. Endémique de Madagascar, il renferme quatre espèces (*S. macrophylla* (R. Vig.) Du Puy & Labat, *S. grandifolia* (R. Vig.) Du Puy & Labat, *S. grandidieri* (Baill.) Du Puy & Labat, et *S. perrieri* (R. Vig.) Du Puy & Labat).

The tribe Millettieae is one of the largest tribes of Papilionoid legumes, along with the Phaseoleae and the Sophoreae (POLHILL 1981); it is diverse and contains numerous species in Madagascar. In order to produce a complete treatment of the Leguminosae-Papilionoideae for Madagascar and the Comoros, we have studied all of the collections of Millettieae from this region held in G, K, MO, P, TAN, TEF and WAG. This research has shown that Madagascar is an important and old centre of diversity for this tribe (LABAT 1996), with 77 specific or subspecific taxa (68 of them endemic) in 10 genera (5 endemic). *Pyranthus* has already been revised for Madagascar (DU PUY & LABAT 1995) and new species and new combinations in *Millettia* Wight & Arnott and *Pongamiopsis* R. Vig. (LABAT & DU PUY 1995) have been published.

GEESINK (1981) isolated a large group of genera within the Millettieae (as "Tephrosieae") with assumed inter-relationships, centred around the large genus *Tephrosia* Pers. (with over 400 species). It included, in addition to *Tephrosia*, the genera *Mundulea* (DC.) Benth. and *Chadsia* Bojer, both of them confined to Madagascar with the exception of *Mundulea sericea* (Willd.) A. Chev. (which is a widespread subspecies occurring from Africa to southern Asia). GEESINK (1984) considered that the position of *Mundulea* needed revision, especially with regard to *Tephrosia*. It appears that *Mundulea* is heterogeneous, and we have described a new genus named *Pyranthus* Du Puy & Labat, which includes 5 species originally described in *Mundulea* or *Tephrosia*, and a single new species (DU PUY & LABAT 1995).

Similarly, *Mundulea macrophylla* R. Vig. must be excluded from the genus *Mundulea* as well as two species described in the genus *Chadsia*, *C. grandifolia* and *C. grandidieri*, since all three species exhibit characters differing from both of these genera: the presence of bracteoles, a distinct hypanthium, a truncate calyx and a cauliflorous habit. In his revision of the genus *Strongylodon*, HUANG (1991) excluded from this genus a very little known species described by VIGUIER (1952) as *Strongylodon perrieri*, on the basis of the leaves lacking stipels, the absence of a discoid nectary and other floral and vegetative characters, without making any suggestion as to its correct classification. It appears that a new genus endemic to Madagascar can be recognised in this complex to accommodate these species: it is described here as *Sylvichadsia*.

Sylvichadsia is characterised by its cauliflorous habit, the presence of bracteoles on the pedicels, its truncate calyx, its wide and distinct hypanthium, its stipitate ovary and its pods which are dehiscent, splitting into 2 spiralling valves. The presence of a hypanthium and bracteoles are considered to be primitive features in the Millettieae, and studies of the evolution of this tribe should include this genus. It has already been demonstrated that the genera *Phylloxylon* and *Vaughania*, also endemic to Madagascar, exhibit some primitive characteristics within the tribe Indigofereae (DU PUY et al. 1994, 1995), and, in cladistic analyses of this tribe, these genera form basal branches of the cladogram (SCHRIRE 1995). *Sylvichadsia* may be similarly basal within the *Millettieae*. The form of the flowers (especially the strongly beaked keel and evenly curved androecium and gynoecium) and the pods of *Sylvichadsia grandifolia* and *S. grandidieri* closely resemble those of *Chadsia*, but they differ in the suberect standard petal and the other characters listed above. The resemblance between the flowers of these two species and those of *Chadsia* can be interpreted as a convergence or parallel evolution of the flowers linked with adaptations to a bird pollination syndrome.

The flowers of *S. macrophylla* are white in colour and most closely resemble those of some *Millettia* species, with a straight androecium and gynoecium sharply upturned at the tip, and a blunt keel tip. However, this species shares all of the generic characteristics listed above (although the pods are not known); its flowers appear different from those of the three other species, but all the differences are linked with the biological specialisation of those other species to bird pollination, and *S. macrophylla* cannot be excluded from *Sylvichadsia*. Its hairy androecium is extremely unusual.

Sylvichadsia perrieri is a liane with trifoliolate

leaves, the flowers are produced in long pseudoracemes and the keel tip has a rather blunt apex. Its habit and leaves are very different from the other species, but the flowers resemble those of *S. grandifolia* and *S. grandidieri*, and they also retain the generic characteristics listed above. Although this species was originally described in the tribe Phaseoleae, it is included here in the genus *Sylvichadsia*. The trifoliolate leaves are very unusual in the Millettieae, although they can be considered as a reduction from imparipinnate leaves. This character occurs in many higher tribes of the Papilionoideae, but it also appears in the tribe Millettieae, in *Disynstemon* R. Vig., a monotypic genus endemic to Madagascar. The vine habit can also be considered as a parallelism appearing in many genera of the tribes Sophoreae and Millettieae, such as in the genera *Baphia* or *Millettia*.

The generic name is derived from "silva/sylva" meaning "forest" and *Chadsia*, another genus in the Millettieae endemic to Madagascar, which has similarly beaked and orange-coloured flowers (especially resembling those of *S. grandifolia* and *S. grandidieri*). *Sylvichadsia* occurs in the humid, eastern rainforests, while *Chadsia* occurs in the seasonally dry, deciduous vegetation of western and southern Madagascar.

SYLVICHADSIA Du Puy & Labat, **gen. nov.**

Arbor, frutex vel liana lignosa, semper cauliflora. Folia imparipinnata vel trifoliolata; stipellae 0. Inflorescentiae in trunco vel in ramis crassissimis dispositae, fasciculatae, racemosae, pseudoracemosae vel paniculatae, bracteolae persistentes in medio vel in ima parte pedicelli dispositae. Flores magnae vel mediocres, 17-45 mm longae, violaceae, rubrae vel albae. Calyx cupularis vel campanulatus, apice truncato edentato vel 4-5 prominentiis minutis proviso; hypanthium latum conspicuumque. Vexillum erectum vel suberectum. Antherae in longitudinem aequantes. Ovarium glabrum, breviter villosum vel pubescens, breve stipitatum, ovulis multis; stigmatum minutum obliquum.

TYPUS.—*Sylvichadsia grandifolia* (R. Vig.) Du Puy & Labat (= *Chadsia grandifolia* R. Vig.).

Cauliflorous trees, shrubs or woody lianes (in *S. perrieri*); deciduous or evergreen. Leaves large, usually clustered on the twig or stem tips, imparipinnate with paired leaflets or pinnately trifoliolate (in *S. perrieri*), glabrous or almost so, glabrescent; stipels absent. Inflorescences from warty growths on the trunk and main branches, the flowers in whorls, racemes, pseudoracemes or panicles; pedicels with a pair of small, persistent bracteoles usually near the middle or in the lower half. Flowers large or medium-sized, 17-45 mm long, purplish to reddish or white (in *S. macrophylla*), the standard with an irregular, whitish basal patch. Calyx cup-shaped to bell-shaped, sometimes narrowly so, not hooded, the apex truncate and without teeth or the teeth reduced to 5 minute points; hypanthium wide and distinct. Standard petal suberect to erect, glabrous or subglabrous behind; wing petals shorter than or as long as and appressed to the keel; keel either extended at the tip into a distinct, narrow beak, or blunt and not beaked (in *S. macrophylla*); androecium and gynoecium shallowly curved to the tip or strongly upcurved apically. Stamens fused into a curved or straight sheath, the outside rarely shortly hairy (in *S. macrophylla*); anthers equal. Ovary shortly stipitate, multi-ovular; style terete or flattened, short-hairy along the inner surface or glabrous (in *S. perrieri*); stigma minute. Pods stipitate, long and narrowly oblong, beaked, splitting into 2 spiralling valves, with several distantly spaced seeds. Seeds not known.

A genus of 4 rare to very rare species confined to the more humid forests of eastern and northern Madagascar. *Sylvichadsia* can be divided into 3 natural groups:

Group 1: Small trees or shrubs; leaves multifoliolate; flowers in fascicles, short racemes, or few-branched panicles; flowers large, 30-45 mm long, red or purplish; keel tip extended into an acute beak; staminal sheath glabrous; androecium and gynoecium evenly curved along their length.—1, *S. grandifolia*; 2, *S. grandidieri*.

Group 2: Shrub; leaves multifoliolate; pseudoracemes short and dense, with numerous flowers in closely spaced clusters along the inflorescence axis; flowers small, 17-20 mm long, white; keel tip rounded, not extended into a beak; staminal

sheath hairy; androecium and gynoecium straight and sharply upturned at the tip.—3, *S. macrophylla*.

Group 3: Liane; leaves 3-foliolate; flowers in long and lax pseudoracemes; flowers medium sized, 22-24 mm long, bright scarlet red; keel tip obtuse, not extended into a long beak; staminal sheath glabrous; androecium and gynoecium evenly curved along their length.—4, *S. perrieri*.

Key to *Sylvichadsia*

1. Shrub or tree; leaves with 5-23 leaflets; flowers in fascicles or in short racemes, panicles or dense pseudoracemes up to 10 cm long; keel tip extended into an acute beak, or if more rounded then flower white (otherwise red or purplish) 2
1'. Liane; leaves with 3 leaflets only; flowers in pseudoracemes ca. 45 cm long; keel tip obtuse, not extended into a beak (flowers bright red) .... 4. **S. perrieri**
2. Flowers smaller, 17-20 mm long, white; keel tip rounded, not extended into a beak; staminal sheath hairy; pseudoracemes dense, with numerous flowers in closely spaced clusters along the inflorescence axis .... 3. **S. macrophylla**
2'. Flowers larger, 30-45 mm long, red or purplish; keel tip extended into an acute beak; staminal sheath glabrous; inflorescences not as above, the flowers in fascicles, short racemes or few-branched panicles 3
3. Calyx cup-shaped, as wide as long or wider; standard 17-30 mm wide; pedicels short, 5-10 mm long; leaves with 5-9 leaflets .... 1. **S. grandifolia**
3'. Calyx tubular, almost twice as long as wide; standard 14-16 mm wide; pedicels 10-20 mm long; leaves with 9-23 leaflets . ... 2. **S. grandidieri**

1. Sylvichadsia grandifolia (R. Vig.) Du Puy & Labat, **comb. nov.**

Chadsia grandifolia R. Vig., Not. Syst., Paris 14: 70 (1950).—Type: *Perrier de la Bâthie 4110*, Sambirano: forêt du Sambirano, Oct. 1908, fl. (lecto-, P; isolecto-, P; chosen here).
Mundulea macrophylla R. Vig., Not. Syst., Paris 14: 67 (1950), pro parte lectotype excl.

A small, evergreen tree or large shrub 4-12 m tall, cauliflorous; trunk reaching 30 cm in diameter, with smooth, greyish bark, releasing a strong, acrid odour when damaged. Leaves in terminal clusters, large, 15-45 cm long, with 5-9 leaflets (2-4 pairs); leaflets large, elliptic to oblong-elliptic, 6-19 × 2.5-9 cm, the apex acuminate and finally obtuse, glabrous, subcoriaceous. Flowers in short racemes or few-branched panicles 0.5-6(-10) cm long with up to ca. 15(-20) flowers, produced from warty outgrowths mostly on the trunk or older branches; pedicels short, 5-10 mm long, with a pair of small bracteoles near the middle or towards the calyx. Flowers 33-45 mm long, deep red or purplish with an irregular, whitish patch at the base of the standard. Calyx wide, cup-shaped, truncate, as wide as long or wider, 7-10 mm long, pubescent to glabrous except for the rim; teeth absent or reduced to 5 very small points on the calyx rim. Standard limb suberect or pointing backwards, widely ovate, 30-40 × 17-30 mm, the apex acute, glabrous, the claw fleshy; wings 6-8 mm wide, slightly shorter than the keel; keel 8-11 mm wide, 45-60 mm long (measured from the base of the claw, around the lower margin to the tip of the beak), sickle-shaped, shallowly but evenly curved along its length, with a short, blunt, upcurved beak. Staminal sheath 25-35 mm long, evenly curved along its length, glabrous. Ovary shortly stipitate; style thinly pubescent along the inner surface. Fruit up to 20 cm long, 15-22 mm wide, flat, appressed-pubescent with short, rust-coloured hairs.—Fig. 1A-G.

VIGUIER cited *Perrier de la Bâthie 18176* and *18190* as syntypes of *Sylvichadsia macrophylla* (as *Mundulea macrophylla*). These two specimens were collected at almost the same locality. However, the inflorescences and flower shapes are very different, and *Perrier de la Bâthie 18190*

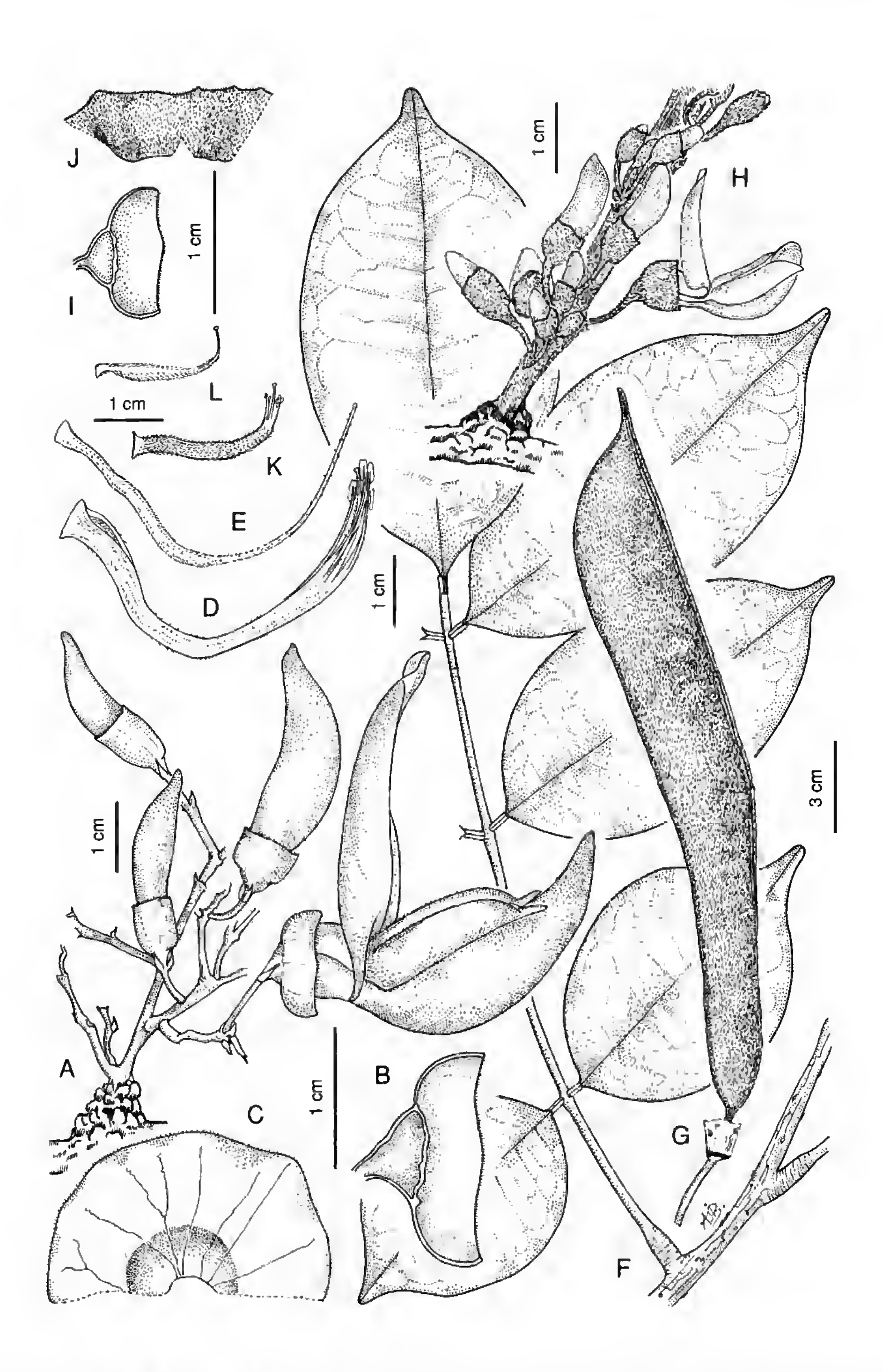


Fig. 1.—A-G, ***Sylvichadsia grandifolia***: **A**, inflorescence (produced from the trunk); **B**, calyx (longitudinal section showing the hypanthium); **C**, calyx exterior; **D**, androecium and style; **E**, gynoecium; **F**, mature leaf; **G**, pod.—H-L, ***Sylvichadsia macrophylla***: **H**, inflorescence (produced from the trunk); **I**, calyx (longitudinal section showing the hypanthium); **J**, calyx exterior; **K**, androecium and style (showing the pubescent staminal sheath); **L**, gynoecium. (A-G, *Service Forestier 9237-SF*; H-L, *Perrier de la Bâthie 18176*).—Drawn by Angela BEAUMONT.

most closely resembles *Sylvichadsia grandifolia* (inflorescence a short spur, flowers large with a beaked keel and wings shorter than the keel, style glabrous, staminal sheath 22-23 mm long and evenly curved along its length). Nevertheless, the whitish flower colour, the presence of a very few hairs on the staminal sheath and the more southerly locality in the same area as *Sylvichadsia macrophylla*, are anomalous and indicate that further collections from eastern Madagascar are needed to clarify the species delimitations and distributions in this genus.

DISTRIBUTION.—NE & N Madagascar, near Antalaha, Andapa, Sambava and Antsirabe [du nord] (300-600 m), and on Montagne d'Ambre (600-1000 m).

HABITAT.—In shaded areas in humid evergreen forest, often near streams or rivers, on acidic (basaltic) soils, at 300-1000 m altitude.

FLOWERING TIME.—September-November.

LOCAL USES.—The wood is soft, brittle, white, with an acrid odour when fresh; all parts of the plant release potent fish toxins upon decomposition.

VERNACULAR NAME.—Fanamo (NE).

MATERIAL EXAMINED.—MADAGASCAR: *Homolle 198*, s.loc., s.d., fl. (P); *Humbert & Capuron 24218*, vallée de l'Andalangy, affluent de l'Androranga (bassin de la Bemarivo du Nord-Est), 300-500 m, 12/14 Nov. 1950, j.fr. (G, K, MO, P, WAG); *Perrier de la Bâthie 18190*, Est: bassin inf. du Mangoro, Oct. 1927, fl., j.fr. (K, P); *Perrier de la Bâthie 18860*, Centre (Nord): Montagne d'Ambre, abondant surtout à la base Est du Pic Badens, ca. 1000 m, Nov. 1932, fl., fr. (K, MO, P); *Réserves Naturelles 8299 RN*, Doany, Andapa, 11 Oct. 1956, fl. (K, P, TEF) ; *Réserves Naturelles 9087 RN Sajy*, Antongondriha, Canton Ambohimitsinjo, Dt. Sambava, 18 Sep. 1957, fl. (P, TEF); *Service Forestier 203 R 152*, Roussette, JB 19, Joffreville, Diégo-Suarez, 630 m, 6 Apr. 1955, st. (K, P); *Service Forestier 811 SF*, bord d'affluent de l'Andalangy (affluent de l'Androranga), Dt. de Sambava, 350-500 m, 12 Nov. 1950, fr. (G, K, MO, P, PRE, TEF); *Service Forestier 9237 SF Capuron*, Est: Forêt d'Andrakaraka (au S-SW d'Antalaha), 20/24 Sep. 1954, fl. (K, P, TEF); *Service Forestier 11283 SF Capuron*, Centre (Nord): massif de la Montagne d'Ambre, 800-900 m, 8/14 Oct. 1954, fl. (B, BR, G, K, MO, P, TEF, WAG); *Service Forestier 24906 SF Capuron*, Est (Nord): Analamanara, près du village de Tsaratanana, entre Antsirabe-Nord et Sambava, 24 Oct. 1966, fr. (K, P, TEF); *Service Forestier 24962 SF Capuron*, Est (Nord): table basaltique d'Ambanitazana, près d'Andrapengy, au N d'Antalaha, 22 Oct. 1966, fl. (K, P, TEF); *Service Forestier 29191 SF Capuron*, Centre (Nord) jusqu'aux confins de l'Ouest (Nord): massif de la Montagne d'Ambre, crête entre les bassins de la rivière des Makis et de la rivière d'Amkazobe, 600-800 m, 26/27 May 1970, fr. (P, TEF); *Ursch 204*, Forêt d'Ambre, Diégo-Suarez, s.d., fl. (K, P).

2. Sylvichadsia grandidieri (Baill.) Du Puy & Labat, **comb. nov.**

Chadsia grandidieri Baill., Bull. Mens. Soc. Linn. Paris 1: 391 (1883), pro parte lectotype incl. (*Grandidier 5*, also cited by BAILLON, is a specimen of *Chadsia flammea*).—Type: *Lantz 22*, Ambakoubé [Ambakobe], 960-1000 m, 16 June (reçu le 22 Feb. 1882), fl. (lecto-, P, chosen here).

A small, evergreen tree or shrub 2.5-3 m tall, cauliflorous. Leaves in terminal clusters, large, 35-52 cm long, with 9-23 leaflets (4-11 pairs); leaflets narrowly elliptic, 6-16 × 1.5-4 cm, the apex acuminate and finally obtuse, completely glabrous. Flowers in fascicles or on very short spurs up to 5 mm long from warty outgrowths on the trunk or older branches; pedicels 10-20 mm long with a pair of minute bracteoles near the middle. Flowers 30-35 mm long, red. Calyx tubular, truncate, almost twice as long as wide, 7-9 mm long, very sparsely appressed-pubescent; teeth almost absent. Standard limb suberect or pointing backwards (folded ca. 5 mm in front of the calyx tip), ovate, ca. 30 × 14-16 mm, the apex acute, glabrous except for a few short hairs near the tip; wings 4-6 mm wide, slightly shorter than the keel; keel narrow, 5-8 mm wide, 42-48 mm long (measured from the base of the claw and around the lower margin to the tip of the keel), sickle-shaped, shallowly and evenly curved, with a short, acute, upturned beak. Staminal sheath ca. 30 mm long, evenly curved, glabrous. Ovary shortly stipitate; style thinly pubescent along the inner surface. Fruit not known.—Fig. 2H-M.

DISTRIBUTION.—SE Madagascar, only known from 2 localities (20-21 km S of Farafangana on the route to Réserve Spéciale de Manombo [0-

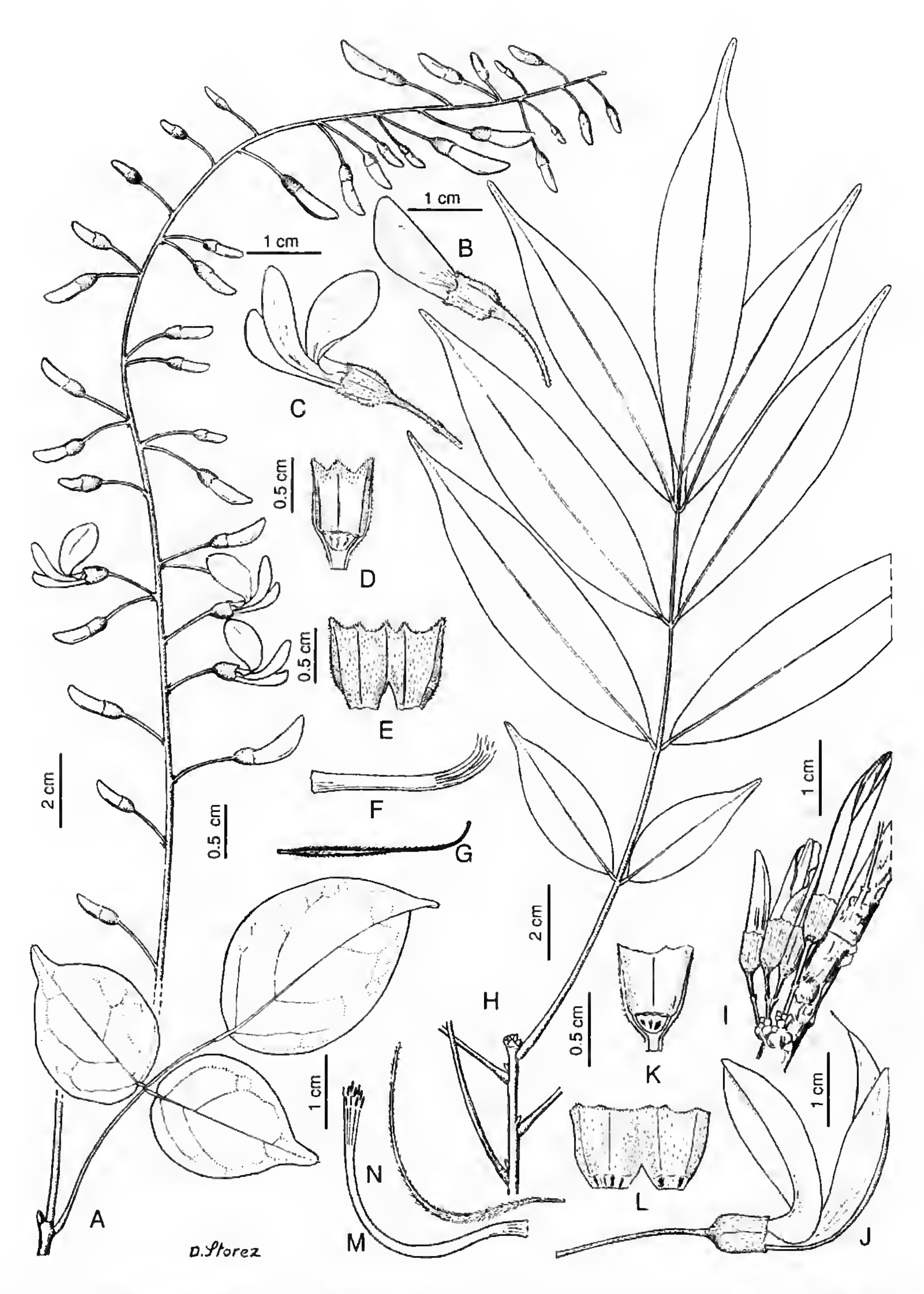


Fig. 2.—A-G, ***Sylvichadsia perrieri***: **A**, mature leaf and inflorescence; **B**, floral bud; **C**, mature flower; **D**, calyx (longitudinal section showing the hypanthium); **E**, calyx exterior; **F**, androecium; **G**, gynoecium.—H-M, ***Sylvichadsia grandidieri***: **H**, mature leaf; **I**, inflorescence (produced from older branches); **J**, mature flower; **K**, calyx (longitudinal section showing the hypanthium); **L**, calyx exterior; **M**, androecium; **N**, gynoecium. (A-G, *Perrier de la Bâthie 18194*; H-J, *Lantz 22*; K-N, *Service Forestier 9207-SF*).—Drawn by Dominique Storez.

130 m altitude], and "Ambakobe" [perhaps Ambatobe near Farafangana?] at 900-1000 m).

HABITAT.—In humid, evergreen forest on lateritic (basaltic) soil or sand, at sea level to 1000 m altitude.

FLOWERING TIME.—Only recorded in June.

MATERIAL EXAMINED.—MADAGASCAR: *Service Forestier 9207 SF Capuron*, Forêt de Manombo, au S de Farafangana, 26 June 1954, fl. (K, P); *Service Forestier 23620 SF Capuron*, Est: au sud de Farafangana, route de Manombo, aux P.K. 20-21, 14/17 Oct. 1964, fl. (P, TEF).

3. Sylvichadsia macrophylla (R. Vig.) Du Puy & Labat, comb. nov.

Mundulea macrophylla R. Vig., Not. Syst., Paris 14: 67 (1950), pro parte lectotype incl. (see also *Sylvichadsia grandifolia*).—Type: *Perrier de la Bâthie 18176*, Est: Bassin inf. du Mangoro, ca. 200 m, Oct. 1927, fl. (lecto-, P; isolecto-, K, P; chosen here).

A shrub 3-4 m tall, cauliflorous. Leaves in terminal clusters, large, 15-25 cm long, with (5-)7-9 leaflets (usually 3 or 4 pairs); leaflets large, elliptic, 5-11 × 2-4.5 cm, the apex shortly acuminate and finally obtuse, thinly appressed-hairy above and beneath at first, glabrescent, becoming coriaceous. Inflorescences dense pseudoracemes up to ca. 10 cm or more long (perhaps longer as the inflorescence matures) produced from the main woody branches, the flowers numerous in dense, closely spaced clusters on short spurs along the main axis; pedicels ca. 8 mm long, with 2 small bracteoles near the middle. Flowers ca. 17-20 mm long, white. Calyx wide, cup-shaped, truncate, as wide as long or wider when mature, ca. 6 mm long, thinly pubescenr; teeth reduced to 5 very small points. Standard limb erect, widely elliptic, ca. 15-18 × 12-17 mm, glabrous; wings ca. 4.5 mm wide, as long as the keel; keel ca. 5.5 mm wide, ca. 20 mm long, slightly curved, the apex rounded (not beaked). Staminal sheath straight, ca. 14-16 mm long, the exterior covered in short, appressed hairs, the apex and the free portion of the filaments upcurved. Ovary shortly stipitate; style short-hairy. Fruit not known.—Fig. 1H-L.

The flowers of this species resemble those of *Millettia* or *Mundulea* (keel short, blunt, not extended into a sharp beak, the ovary and staminal tube straight, with the style and free portion of the filaments strongly upcurved). Nevertheless, the cauliflorous habit, the leaf and leaflet size, the presence of bracteoles and an hypanthium, the truncate calyx and the stipitate ovary closely resemble *Sylvichadsia grandifolia*, and there can be no doubt that they are closely related.

DISTRIBUTION.—E Madagascar, known only from the type locality in the lower Mangoro River basin (ca. 20°S-48°30'E).

HABITAT.—Remnants of humid, evergreen, eastern forest, at ca. 200 m altitude.

FLOWERING TIME.—October.

4. Sylvichadsia perrieri (R. Vig.) Du Puy & Labat, comb. nov.

Strongylodon perrieri R. Vig., Not. Syst., Paris 14: 175 (1952).—Type: *Perrier de la Bâthie 18194*, Est: Bassin inf. du Mangoro, ca. 200 m, Oct. 1927, fl. (holo-, P; iso-, P).

A woody liane; stems short-hairy when young, soon glabrescent; stipels absent. Leaves pinnately 3-foliolate; leaflets (25-)45-90 × (15-)25-55 mm, rounded at the base, shortly tapering apically, glabrous and glossy above, with a few hairs especially on the veins beneath, becoming entirely glabrous, coriaceous; stipules narrowly triangular, becoming rigid. Pseudoracemes ca. 45 cm long, the axes finely hairy with short, erect, rusty or red-brown hairs, the flowers numerous mostly in clusters of 3 on swollen nodes along the axis; pedicels 10-15 mm long, hairy with a pair of minute bracteoles inserted in the lower half. Flowers 22-24 mm long, bright scarlet-red including the calyx. Calyx bell-shaped, 5-6 mm long, thinly pubescent outside, pubescent within, with a distinct hypanthium; teeth 4, very small, triangular, the upper tooth notched. Standard limb erect, oblong-elliptic ca. 19-20 × 12-13 mm, notched apically, glabrous, auriculate but without basal appendages, with a claw ca. 6 mm long; wings as long as the keel, the limb narrowly

oblong, ca. 18 × 4.5 mm, auriculate basally, with pubescent margins towards the base; keel curved, ca. 19 × 6 mm, obtuse (not beaked), auriculate and pubescent towards the base. Staminal sheath curved, ca. 17 mm long, glabrous. Ovary shortly stipitate, hairy, with ca. 12 ovules; style slender, flattened, glabrous except near the base. Pods not known.—Fig. 2A-G.

DISTRIBUTION.—Only known from the lower Mangoro River valley in E Madagascar.

HABITAT.—In remnants of humid, eastern, lowland forest, at ca. 200 m altitude.

FLOWERING TIME.—Only recorded in October.

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Impact des feux de brousse sur les maquis ligno-herbacés des roches ultramafiques de Nouvelle-Calédonie

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RÉSUMÉ
L'effet des feux de brousse sur deux catégories de maquis ligno-herbacés, se développant sur sols issus de roches ultramafiques, a été suivi sur une période de plus de 10 ans, par la méthode des points quadrats. Au terme des observations, on assiste à la reconstitution presque complète du cortège floristique initial. La majorité des espèces arbustives se régénèrent par rejets. Toutefois cinq espèces ne se réinstallent que très progressivement, par germinations de semences. Le changement le plus important est d'ordre structural et intervient au niveau de la strate herbacée. Les Cyperaceae cespiteuses, entièrement détruites par l'incendie, ne se réinstallent que très lentement à partir de semences. L'espace laissé libre est largement occupé par une espèce jonciforme rhizomateuse (*Lepidosperma perteres*) qui, contrairement aux Cyperaceae précédentes, s'oppose à la progression du feu. La reconstitution du tapis végétal après incendie s'apparente donc a une « autosuccession » qui permet au maquis, si aucun facteur n'intervient pour provoquer un nouvel incendie, de retrouver à terme ses caractéristiques initiales. Toutefois, l'interruption du processus de reconstitution par un incendie précoce, entraîne une prolifération de *Pteridium esculentum*. Cette espèce, très inflammable, favorise la propagation du feu dont les effets répétés se traduisent par l'installation d'une fougeraie permanente.

MOTS CLÉS
incendies,
maquis,
roches ultramafiques,
flore endémique,
Cyperaceae,
autosuccession,
Nouvelle-Calédonie.

ABSTRACT

The effect of fire on two types of woody-herbaceous maquis on soils derived form ultramafic rocks was examined for over ten years using the line transect method. During the course of the study, the initial floristic composition was almost completely restored. Most of the woody species resprout, whereas five fire sensitive species reestablish slowly on burnt areas from seed. The most important change was structural, taking place in the herbaceous layer. Tussock Cyperaceae, entirely eliminated by the fire, regrew very slowly from seed. Open areas were largely occupied by a single rhizomatous species (*Lepidosperma perteres*) which, unlike the Cyperaceae present before burning, is resistant to the spread of fire. The formation of a new plant cover after burning thus represents "autosuccession", enabling the maquis to return to its initial characteristics provided that no additional fires occur. This process of vegetation recovery can however be interrupted by premature burning, which brings about a proliferation of *Pteridium esculentum*, a highly flammable species that facilitates the spread of fire. Repeated burning can thus result in the establishment of a permanent fern cover.

KEY WORDS
fire,
maquis,
ultramafic rock,
endemic flora,
Cyperaceae,
autosuccession,
New Caledonia.

INTRODUCTION

Les feux de brousse constituent dans l'ensemble du monde tropical et méditerranéen, comme en témoignent de nombreux ouvrages (GILL et al. 1981 ; BOOYSEN & TAINTON 1984 ; GOLDAMMER 1990 ; VAN WILGEN et al. 1992 ; WHELAN 1995), l'un des facteurs principaux de dégradation et de transformation du milieu naturel. Ceci est également le cas, en Nouvelle-Calédonie, où, comme souligné par VIROT (1956) les feux de brousse ont eu un rôle important dans la configuration et la distribution actuelles des formations végétales.

On peut à ce jour estimer que la totalité des savanes, des fourrés et des maquis sur roches acides, soit un total de 6500 km^2, en sont le résultat. Ces formations, dont la flore est composée majoritairement d'espèces introduites, ont été classées par MORAT et al. (1981) en « formations transformées ». Elles s'opposent aux « formations autochtones » dont la flore est très largement constituée d'espèces endémiques de la Nouvelle-Calédonie. Ceci n'exclut pas que certaines formations autochtones de type édaphique comme les « maquis miniers » résultent pour la plupart de la destruction du couvert forestier initial (JAFFRÉ 1980 ; MORAT et al. 1986). — Fig. 1.

Bien que l'on ait tendance à considérer que les feux ont débuté avec l'arrivée de l'homme, estimée à environ 4000 BP pour la Nouvelle-Calédonie, des études récentes (HOPE, sous presse), basées sur l'examen de pollens fossiles recueillis dans des sédiments anciens de la Plaine des Lacs, remettent en cause ce point de vue. Les résultats montrent l'alternance depuis 30.000 ans de phases forestières et de phases pionnières « post incendie » marquées localement par la dominance d'espèces pionnières du genre *Gymnostoma* (Casuarinaceae). L'adaptation au feu des espèces néo-calédoniennes pourrait donc être beaucoup plus ancienne que ce que l'on a coutume de considérer.

La gravité des atteintes provoquées par des feux de brousse au couvert végétal actuel, est largement fonction des caractéristiques des groupements végétaux touchés (JAFFRÉ et al. 1997). Aussi une meilleure connaissance des effets immédiats et à plus long terme, des incendies sur les différentes catégories de végétation, est-elle nécessaire pour définir les modalités de gestion, adaptées à chaque cas.

Si la foudre peut être à l'origine de quelques foyers, il est certain que les incendies se sont intensifiés depuis l'arrivée des premiers hommes en Nouvelle-Calédonie (estimée à 4000 BP) et sont largement liés aux pratiques culturales. Les feux sont utilisés comme auxiliaires nécessaires au défrichement des terres destinées à l'agriculture et, depuis l'arrivée des Européens, à l'élevage. Ils se sont accrus aux cours des dernières décennies avec le développement économique du Territoire et l'ouverture de nouvelles voies d'accès. Dans les secteurs sans valeur agricole, les feux sont associés à des pratiques de chasse et à des prospections minières et aussi, bien souvent, à la propagation accidentelle non contrôlée des feux allumés initialement pour défricher des zones à vocation agro-pastorale. Toutefois beaucoup d'incendies, qui n'ont pas de causes identifiées, sont dus à des négligences et à des actes de malveillance.

CADRE ET MÉTHODES D'ÉTUDE

Cette étude concerne l'effet des incendies sur une catégorie de « maquis minier », le « maquis ligno herbacé » et a pour but, d'une part d'évaluer la nature, l'importance et la durée des modifications du couvert végétal, d'autre part d'analyser le processus de sa reconstitution.

Le terme de « maquis minier » dans son acception locale « regroupe toutes les formations sur roches ultramafiques (péridotites et serpentinites) n'appartenant pas à la forêt dense humide ou aux forêts rivulaires. Il regroupe des formations sclérophylles sempervirentes héliophiles, arbustives plus ou moins buissonnantes ou ligno-herbacées à strate cypéracéenne dense » (MORAT et al. 1986). Ces dernières, qui sont les seules concernées par la présente étude, occupent des zones anciennement boisées. Leur flore est constituée, comme celle de l'ensemble des maquis miniers,

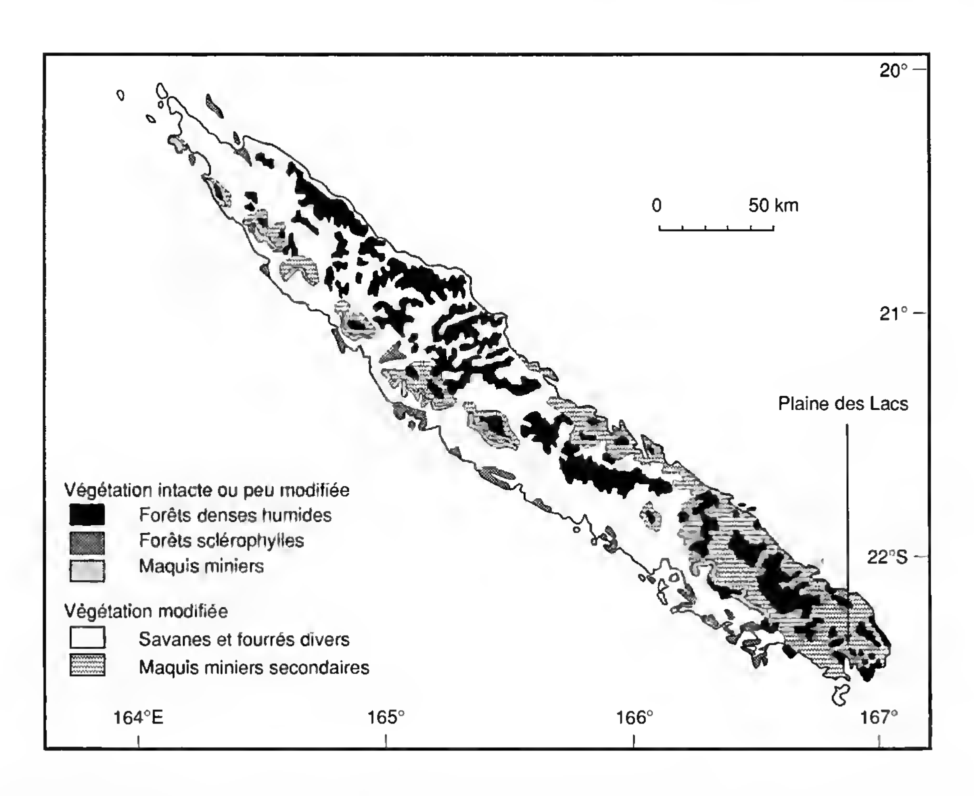


Fig. 1. — Répartition des principales formations végétales de la Grande-Terre (Nouvelle-Calédonie), et localisation du secteur de la Plaine des Lacs.

par un fort pourcentage (entre 85 et 90%) d'espèces endémiques du Territoire (JAFFRÉ et al. 1994).

Les maquis ligno-herbacés sur roches ultramafiques se distinguent des autres catégories de maquis par une strate herbacée très développée (recouvrement > 75%). Celle ci est formée en majorité de Cyperaceae cespiteuses appartenant aux genres *Costularia* et *Schoenus*, très inflammables en période sèche et d'une espèce jonciforme plus discrète, *Lepidosperma perteres*. Le taux de recouvrement de la strate herbacée est supérieur à celui de la strate arbustive qui peut être buissonnante et discontinue d'une hauteur comprise entre 20 cm et 1,3 m.

Ce type de maquis se trouve sur sols oxydiques (ferrallitiques ferritiques) remaniés par érosion et colluvionnement sur les versants ou en situation de piémont à des altitudes variées, du niveau de la mer à 1600 m d'altitude. Il ne se trouve pas sur les sols oxydiques cuirassés ou gravillonnaires peu propices au développement des Cyperaceae. L'effet des incendies sur les maquis occupant ces derniers substrats a été étudié séparément (MAC COY et al., sous presse ; RIGG et al., sous presse).

L'étude a débuté en octobre 1984, trois semaines après le passage du feu. Elle porte sur un maquis de piémont et un maquis de haut versant de la Plaine des Lacs (Fig. 1) situés entre 230 et 260 m d'altitude, à l'extrême sud de la Grande-Terre. La pluviométrie annuelle moyenne de la zone s'établit entre 2500 et 3000 mm. Les mois les plus secs, avec des précipitations inférieures à 100 mm, se situent de manière assez irrégulière de septembre à novembre. La température annuelle moyenne est de l'ordre de 21°, le mois le plus chaud étant février (25°) et le mois le plus frais, août (18°).

En se référant aux travaux antérieurs réalisés dans le Grand Massif du Sud (JAFFRÉ 1980) il est possible de rattacher le maquis de haut versant à l'association à *Costularia pubescens* et *Styphelia albicans*, le maquis de piémont à l'association à *Codia discolor* et *Eugenia stricta*. Dans les deux cas, il s'agit d'une végétation peu dynamique constituée d'espèces adaptées à des conditions de nutrition minérale extrêmes en raison de la pauvreté du sol en P, K et Ca et à des teneurs anormalement élevées en nickel, chrome et manganèse (Tableau 1).

TABLEAU 1. — Composition chimique moyenne de l'horizon supérieur (2-10 cm) des sols de hauts versants et des sols de piémonts.

	Stations	
Analyses	Haut versant	Piémont
pH	6,2 ± 1,4	5,4 ± 0,5
Bases échangeables (me / 100 g)		
Ca^{++}	0,85 ± 0,53	0,37 ± 0,34
Mg^{++}	1,54 ± 1,02	0,46 ± 0,38
K^{+}	0,05 ± 0,02	0,05 ± 0,03
Na^{+}	0,07 ± 0,02	0,05 ± 0,03
Éléments totaux		
P ppm	227 ± 175	241 ± 143
Ca %	0,01 ± 0,01	0,01 ± 0,00
Mg %	0,65 ± 0,38	0,33 ± 0,28
K %	0,02 ± 0,02	0,02 ± 0,02
Na %	0,04 ± 0,04	0,04 ± 0,06
Mn %	0,45 ± 0,17	0,63 ± 0,37
Ni %	0,96 ± 0,21	0,68 ± 0,22
Cr %	2,5 ± 1,5	2,4 ± 1,1
Fe %	41,7 ± 8,0	46,1 ± 3,8

En raison de l'importance des Cyperaceae cespiteuses et stolonifères pour lesquelles la notion d'individu est souvent ambiguë, l'évolution du tapis végétal a été suivie par la méthode linéaire des points quadrats (CANFIELD 1941) dont la technique a été reprise et décrite pour une étude similaire par FORGEARD & TOUFFET (1979).

Chaque ligne élémentaire a été matérialisée sur le terrain par 2 piquets entre lesquels est tendue une cordelette à laquelle est superposé un ruban métallique gradué. Les lectures ont été effectuées tous les 10 cm à différentes périodes, de la date de l'incendie à 1997 pour la zone de haut versant et seulement jusqu'en 1995 pour la zone de piémont, qui en 1996 à été défrichée pour une opération de reboisement.

Le principe de la méthode consiste à noter les espèces touchant une tige métallique de faible diamètre plantée perpendiculairement au sol. Les données recueillies permettent de calculer à un temps donné :

— le recouvrement végétal, qui correspond au pourcentage de points où une ou plusieurs espèces sont en contact avec la tige de mesure ;

— la fréquence relative des diverses espèces, représentée par le pourcentage de points de lecture où l'espèce est notée ;

— la contribution spécifique des diverses espèces, qui est le rapport de la fréquence relative d'une espèce à la somme des fréquences relatives de toutes les espèces.

En outre, toutes les espèces ont été inventoriées sur 2500 m² de la zone brûlée et des plants des différentes espèces ont été déterrés afin de déterminer leurs modes de régénération et de multiplication.

Dans chacune des deux zones, les lignes permanentes ont été établies au sein de surfaces homogènes représentatives de l'ensemble ; elles totalisent 170 m (6 lignes de 25 m et une ligne de 20 m) en position de haut versant et 150 m (6 lignes de 25 m) en zone de piémont.

RÉSULTATS

Évolution de la composition et de la richesse floristique

La comparaison de la composition floristique initiale et de celle observée au terme de 13 ans pour le haut versant et de 11 ans pour le piémont montre une grande stabilité. En effet, 44 espèces sur les 46 initiales se retrouvent dans la parcelle de haut versant et 40 sur 41 dans celle de piémont (Tableau 2).

On note seulement la disparition de *Myodocarpus lanceolatus* (Araliaceae) dans les deux stations et celle de *Styphelia albicans* (Epacridaceae) dans le maquis de haut versant. L'absence de *Myodocarpus lanceolatus* s'explique par son caractère pré-forestier, commun à plusieurs espèces de la famille des Araliaceae de la flore de Nouvelle-Calédonie. L'absence de *Styphelia albicans* tient à la lenteur de la plupart des espèces du maquis minier à se réinstaller à partir de semences. Ainsi *Styphelia cymbulae* et *Dracophyllum ramosum*, deux autres espèces de la famille des Epacridaceae qui ne rejettent pas de souche, n'ont été observées respectivement sur les lignes de lecture que 5 et 7 années après l'incendie.

Les espèces supplémentaires ne sont qu'au nombre de deux, *Baumea deplanchei* (Cyperaceae) (espèce pionnière des surfaces nues, endémique des sols issus de roches ultramafiques), commune aux deux stations, et *Pinus caribaea* (espèce introduite, plantée dans le secteur en 1965) dont trois individus se sont installés dans la parcelle de piémont, où il montre toutefois un développement limité. L'observation de maquis miniers n'ayant pas brûlé depuis plusieurs dizaines d'années permet de constater que *Baumea deplanchei* ne persiste pas lorsque la strate herbacée, à base de Cyperaceae cespiteuses, est redevenue dense. Par contre *Pinus caribaea* demeure et devient parfois envahissant, notamment dans les zones de piémont à proximité des plantations.

Évolution du taux de recouvrement végétal

L'évolution du taux de recouvrement de la végétation, dans chacune des stations étudiées, est représentée sur la Figure 2.

On observe dans les deux cas une reprise rapide de la végétation qui, d'une manière générale, débute dès la première pluie après l'incendie. Bien que le haut versant soit l'objet d'une érosion consécutive au feu, son recouvrement végétal

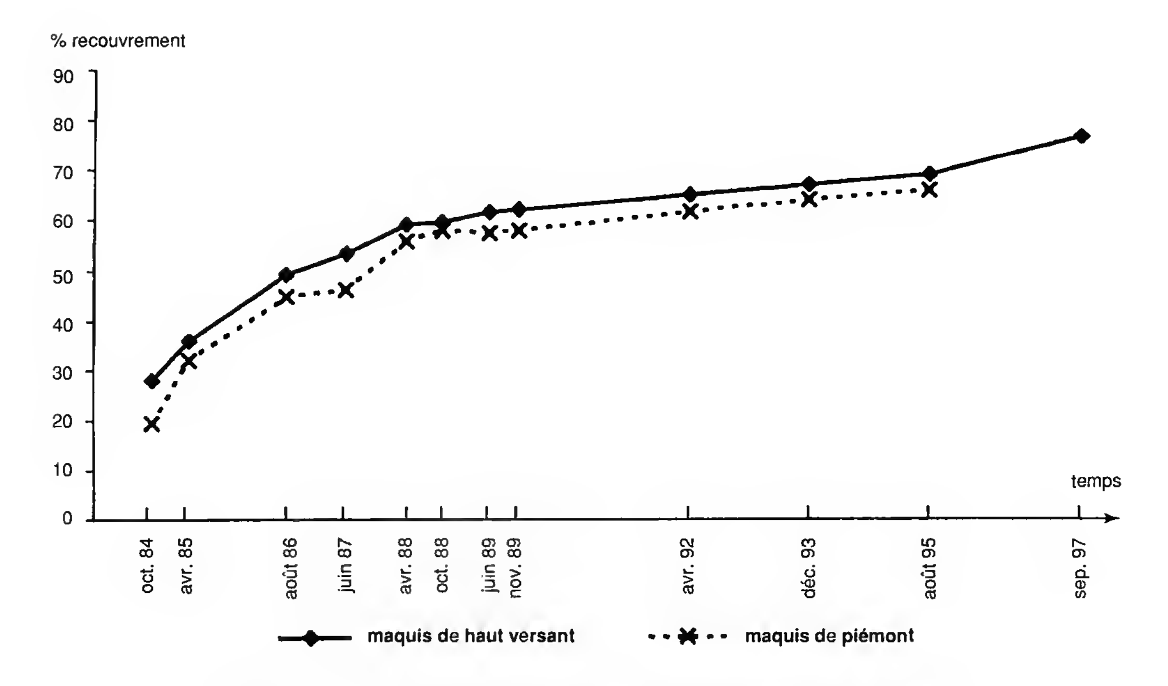


Fig. 2. — Évolution du taux de recouvrement de la végétation des deux stations étudiées.

demeure supérieur à celui du piémont. Les taux de recouvrement croissent rapidement au cours des deux premières années et marquent un fléchissement à partir de la quatrième année. Sur haut versant, les zones dénudées correspondent à des blocs rocheux et à de petites ravines d'érosion qui se creusent à chaque forte pluie. Sur piémont ce sont des plages de gravillons, inondées en période de pluies abondantes et arides en période sèche. Les taux de recouvrement mesurés au terme des observations (environ 75% sur haut versant et 60% sur piémont) sont assez proches de ceux généralement observés pour les maquis ligno-herbacés voisins, épargnés par le feu depuis plusieurs décennies. Toutefois la végétation demeure dans les deux zones étudiées, moins haute et moins dense en raison d'une faible superposition des frondaisons des différentes espèces.

Évolution des composantes de la végétation

En fonction de leur morphologie et de leur dynamique, on peut distinguer 5 composantes de la végétation :

— *Pteridium esculentum*, fougère rhizomateuse, très discrète et souvent absente des maquis épargnés par le feu depuis plusieurs décennies, qui émet de nombreuses frondes après l'incendie ;

— *Lepidosperma perteres*, Cyperaceae, espèce jonciforme rhizomateuse, très clairsemée dans la végétation initiale, qui émet d'abondantes tiges après incendie ;

— L'ensemble des Cyperaceae cespiteuses, qui constituaient la plus grande partie du couvert herbacé (recouvrement de l'ordre de 75%) et de la biomasse facilement combustible avant l'incendie.

— L'ensemble des espèces arbustives, dont le recouvrement était compris entre 30 et 50% avant l'incendie ;

— L'ensemble des espèces n'appartenant pas aux catégories précédentes : *Dianella stipitata* (Liliaceae), *Eriaxis rigida* et *Megastylis gigas* (Orchidaceae), *Schizaea dichotoma* et *S. laevigata* (Schizaeaceae), dont la somme des importances relatives n'excède à aucun moment 2,75% et dont les variations sont, compte tenu des marges d'erreur, trop faibles pour être interprétées.

% fréquence relative

60
50
40
30
20
10
0

Maquis de haut versant

oct. 84
avr. 85
août 86
juin 87
avr. 88
oct. 88
juin 89
nov. 89
avr. 92
déc. 93
août 95
sep. 97

Pteridium esculentum
Lepidosperma perteres
Cyperaceae cespiteuses
Ensemble des espèces arbustives

Fig. 3. — Évolution de la fréquence relative des quatre principales composantes de la végétation sur haut versant.

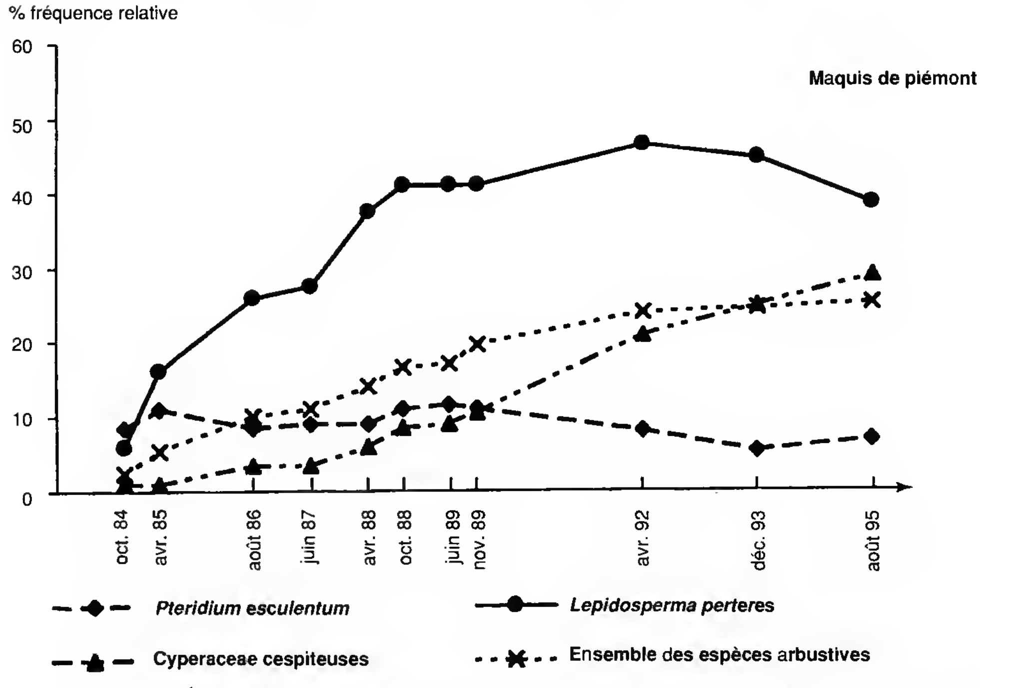


Fig. 4. — Évolution de la fréquence relative des quatre principales composantes de la végétation sur piémont.

% contribution spécifique

Maquis de haut versant

70
60
50
40
30
20
10
0

oct. 84
avr. 85
août 86
juin 87
avr. 88
oct. 88
juin 89
nov. 89
avr. 92
déc. 93
août 95
sep. 97

Pteridium esculentum
Lepidosperma perteres
Cyperaceae cespiteuses
Ensemble des espèces arbustives

Fig. 5. — Évolution de la contribution spécifique des quatre principales composantes de la végétation sur haut versant.

% contribution spécifique

Maquis de piémont

70
60
50
40
30
20
10
0

oct. 84
avr. 85
août 86
juin 87
avr. 88
oct. 88
juin 89
nov. 89
avr. 92
déc. 93
août 95

Pteridium esculentum
Lepidosperma perteres
Cyperaceae cespiteuses
Ensemble des espèces arbustives

Fig. 6. — Évolution de la contribution spécifique des quatre principales composantes de la végétation sur piémont.

L'évolution de la fréquence relative des quatre principales composantes de la végétation est représentée sur la Figure 3 pour la station de haut versant et sur la Figure 4 pour celle de piémont. L'évolution de la contribution spécifique est pour sa part représentée sur la Figure 5 pour le maquis de haut versant et sur la Figure 6 pour celui de piémont.

— Évolution de *Pteridium esculentum.*

Dans chacune des stations, l'installation de cette espèce est immédiate, puisqu'elle émet de nouvelles frondes très rapidement après l'incendie. Ses fréquences relatives, de 15% sur haut versant et d'environ 10% sur piémont, données dès la première lecture, demeurent relativement stables au cours des 4 à 5 premières années d'observation. Elle décroît ensuite sensiblement pour atteindre finalement des valeurs de 3% sur haut versant après 13 ans et de 5% sur piémont au bout de 11 ans.

Pteridium esculentum présente la contribution spécifique la plus importante 3 semaines après l'incendie. Elle s'érablit à 44% sur piémont et 65% sur haut versant. Mais elle décroît ensuite rapidement, surtout les deuxième et troisième années et atteint finalement dans les deux cas, une valeur en dessous de 10% au bout d'une dizaine d'années, soit la valeur la plus basse des 4 composantes principales du couvert végétal.

— Évolution de *Lepidosperma perteres.*

La fréquence relative de cette espèce joneiforme, qui émet d'abondantes tiges dès les premières semaines suivant l'incendie, ne cesse de croître pendant les 5 à 8 premières années pour atteindre respectivement 45% et 50% sur piémont et sur haut versant. Au cours des années suivantes on note un fléchissement de la courbe qui atteint finalemenr dans les deux cas une valeur voisine de 40%.

Lepidosperma perteres possède, dès les premiers mois sur piémont et au bour de moins de 2 ans sur haut versant, une contribution spécifique supérieure à celle des autres composantes de la végétation. Sur haut versant la valeur de la contribution spécifique reste relativement stable entre 2 et 5 ans puis décroît progressivement, à partir de la cinquième année. Sur piémont cette décroissance est sensible dès la quatrième année. Dans chacun des cas elle atteint, au terme des observations, des valeurs voisines de 40%. À ce stade, la contribution spécifique de *Lepidosperma perteres* est égale ou supérieure à celle des autres composantes de la végétation mais se trouve dans une phase décroissante alors que la contribution spécifique des autres composantes est dans une phase croissante.

La prépondérance de *Lepidosperma perteres,* qui occupe l'espace laissé libre par la destruction des Cyperaceae cespiteuses, donne aux deux maquis étudiés une physionomie particulière (« maquis joneiforme ») qui, sur le terrain, permet aisément d'identifier les zones ayant brûlé il y a 5 à 10 ans.

— Évolution de l'ensemble des espèces arbustives.

La fréquence relative des espèces arbustives, dont le plus grand nombre rejette de souche après l'incendie, plus ou moins rapidement selon les conditions hydriques liées à la pluviométrie, croît assez régulièrement au cours des périodes d'observation. Elle atteint 23% en zone de piémont et 35% sur haut versant au bout, respectivement, de 11 et 13 ans.

La contribution spécifique des espèces arbustives croît lentement dans les deux stations. Elle atteint 24% en zone de piémont et 28% en position de haut versant après 11 années et 35% sur haut versant après 13 ans. Dans ce dernier cas, la contribution spécifique des espèces arbustives, en phase croissante, est égale à celle de *Lepidosperma perteres.*

— Évolution de l'ensemble des Cyperaceae cespiteuses.

La strate de Cyperaceae cespiteuses (*Costularia, Schoenus*), la plus vulnérable au feu, ne subsiste après l'incendie qu'à l'état de touffes isolées localement épargnées par les flammes. Sa réinstallation s'effectue très lentement par semences au cours des 4 à 6 premières années suivant l'incendie et s'amplifie ensuite, de manière plus nette sur piémont que sur haut versant. Au terme des observations sa fréquence relative, en phase croissante, atteint 30% sur piémont et 25% sur haut versant.

La contribution spécifique des Cyperaceae cespiteuses demeure inférieure à celle des 3 autres principales composantes de la végétation jusqu'à la cinquième année sur piémont et jusqu'à la huitième année sur haut versant, atteignant dans

chaque cas une valeur de l'ordre de 10%. Ensuite, elle s'accroît plus rapidement sur piémont que sur haut versant. Elle atteint dans le premier cas une valeur de 28% au bout de 11 ans et se situe en deuxième position juste en dessous de *Lepidosperma perteres*. Dans le second cas elle atteint 18% la onzième année et 25% au bout de 13 ans. À ce stade elle se trouve en troisième position, en dessous de *Lepidosperma perteres* et de l'ensemble des espèces arbustives.

Réaction des espèces à l'action du feu

Les modes de réinstallation des différentes espèces observées dans les deux stations sont donnés dans le Tableau 2.

Peu d'espèces meurent massivement après l'incendie. C'est toutefois le cas, comme il a été noté plus haut, des Cyperaceae cespiteuses, notamment de *Costularia nervosa* et à un degré moindre de *Costularia comosa*, *C. stagnalis*, *C. arundinacea*, *Schoenus neocaledonicus* et *Sch. juvenis*. C'est aussi le cas de quelques espèces arbustives : *Dracophyllum ramosum*, *Styphelia cymbulae* et *S. albicans* (Epacridaceae), *Myodocarpus lanceolatus* (Araliaceae) et *Alphitonia neocaledonica* (Rhamnaceae). Ces différentes espèces ne se réinstallent ensuite qu'à partir de graines. Dans le cas des Cyperaceae comme dans celui d'*Alphitonia neocaledonica*, la régénération s'effectue à partir de semences contenues dans le sol

TABLEAU 2. — Composition floristique et modes de réinstallation des espèces des deux parcelles étudiées.

	Espèces	Piémont	Haut versant	Mode de réinstallation
	Agavaceae			
	Cordyline neocaledonica Linden		X	R
	Apocynaceae			
	Melodinus balansae Baill.	X		R
	Parsonsia populifolia Baill.		X	R
	Araliaceae			
♦	*Myodocarpus lanceolatus* Dubard & R. Vig.	X	X	S
	Asclepiadaceae			
	Marsdenia microstoma Schltr.		X	R
	Celastraceae			
	Peripterygia marginata (Baill.) Loes.	X	X	R
	Cunoniaceae			
	Codia discolor (Brongn. & Gris) Guillaumin	X		R
	Codia nitida Schltr.	X	X	R
	Pancheria alaternoides Brongn.	X	X	R
	Pancheria hirsuta Vieill. ex Pamp.	X		R
	Pancheria vieillardii Brongn.	X		R
	Cyperaceae			
•	*Baumea deplanchei* Boeck.	X	X	S
	Costularia arundinacea (Sol. ex Vahl) Kük.		X	S
	Costularia comosa (CB. Clarke) Kük.	X		S
	Costularia nervosa J. Raynal	X	X	S
	Costularia pubescens J. Raynal		X	S
	Costularia stagnalis (Däniker) Kük.	X		S
	Lepidosperma perteres C.B. Clarke	X	X	R
	Schoenus juvenis C.B. Clarke		X	S
	Schoenus neocaledonicus C.B. Clarke	X	X	S
	Dennstaedtiaceae			
	Pteridium esculentum (Forster f.) Cockayne	X	X	R
	Dilleniaceae			
	Hibbertia pancheri (Brongn. & Gris) Briq.		X	R
	Hibbertia pulchella (Brongn. & Gris) Schltr.	X	X	R
	Hibbertia trachyphylla Schltr.		X	R
	Epacridaceae			
♦	*Styphelia albicans* (Brongn. & Gris) Sleumer		X	S

Styphelia cymbulae (Labill.) Sprengel	X	X	S
Dracophyllum ramosum Pancher ex Brongn. & Gris	X	X	S
Escalloniaceae			
Argophyllum montanum Schltr.		X	R
Euphorbiaceae			
Phyllanthus aeneus Baill.	X	X	R
Phyllanthus chrysanthus Baill.		X	R
Flacourtiaceae			
Casearia silvana Schltr.	X	X	R
Goodeniaceae			
Scaevola beckii Zahlbr.	X	X	R S
Guttiferae			
Garcinia amplexicaulis Vieill.	X	X	R
Montrouziera sphaeroidea Pancher ex Planch. & Triana	X	X	R
Liliaceae			
Dianella stipitata Schlittler	X	X	R
Linaceae			
Hugonia penicillanthemum Baill. ex Pancher & Sebert		X	R
Loganiaceae			
Geniostoma celastrineum Baill.	X	X	R
Moraceae			
Ficus aspera G. Forst.		X	R
Myrtaceae			
Austromyrtus alaternoides (Brongn. & Gris) Burret		X	R
Babingtonia leratii (Schltr.) A.R. Beans	X	X	R
Cloezia artensis (Montr.) P.S. Green	X	X	R
Eugenia stricta Pancher ex Brongn. & Gris	X		R
Tristaniopsis glauca Brongn. & Gris	X	X	R
Uromyrtus emarginata (Pancher ex Brongn. & Gris) Burret	X	X	R
Xanthostemon aurantiacum (Brongn. & Gris) Schltr.	X		R
Orchidaceae			
Enaxis rigida Reichb. f.	X	X	R
Megastylis gigas (Reichb. f.) Schtr.	X	X	R
Pinaceae			
• *Pinus caribaea* Morelet	X		S
Proteaceae			
Grevillea exul Lindley subsp. *rubiginosa* (Brongn. & Gris) Virot		X	R
Grevillea gillivrayi Hook. & Arn.	X		R
Stenocarpus umbelliferus (J.R. Forst.) Druce	X		R
Rhamnaceae			
Alphitonia neocaledonica (Schltr.) Guillaumin	X		S
Rubiaceae			
Normandia neocaledonica Hook. f.		X	R
Psychotria oleoides (Baill.) Schltr.	X		R
Sapindaceae			
Guioa glauca (Labill.) Radlk.	X	X	R
Guioa villosa Radlk.	X	X	R
Storthocalyx pancheri (Baill.) Radlk.		X	R
Schizaeaceae			
Schizaea dichotoma (L.) Smith	X	X	R
Schizaea laevigata Mett.		X	R
Smilacaceae			
Smilax sp. (Veillon 6882)		X	R
Thymeliaceae			
Wikstroemia indica (L.) C. Meyer	X		R
Violaceae			
Agatea deplanchei Brongn. & Gris ex Guillaumin	X		R

• espèce n'appartenant pas à la flore initiale — R rejets
♦ espèce non répertoriée au terme des observations — S semences

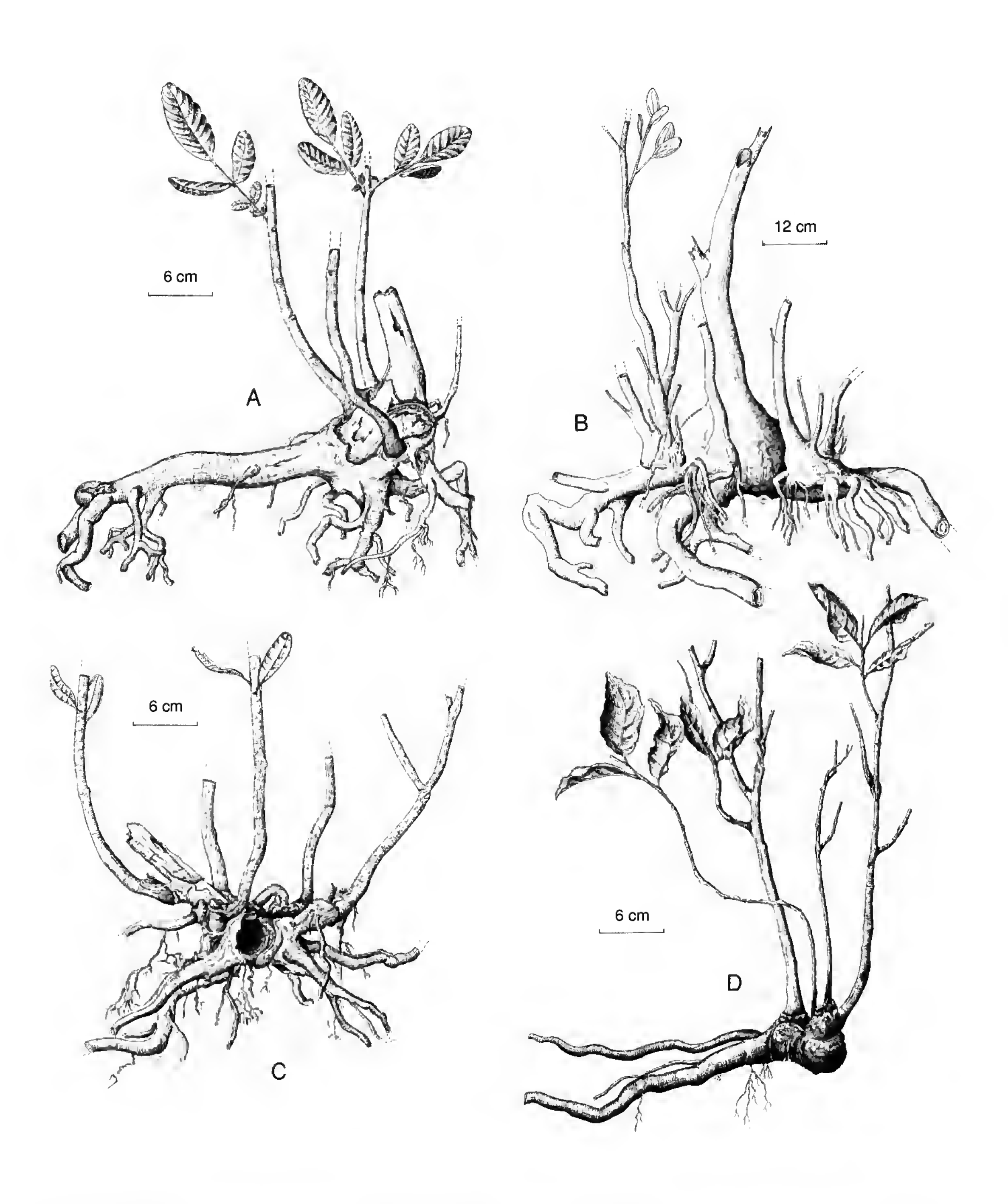


Fig. 7. — Exemples de bourrelets ligneux (lignotuber) chez quelques espèces du maquis ligno-herbacé sur roches ultramafiques : **A**, ***Pancheria hirsuta*** ; **B**, ***Stenocarpus umbelliferus*** ; **C**, ***Xanthostemon aurantiacum*** ; **D**, ***Agatea deplanchei***.

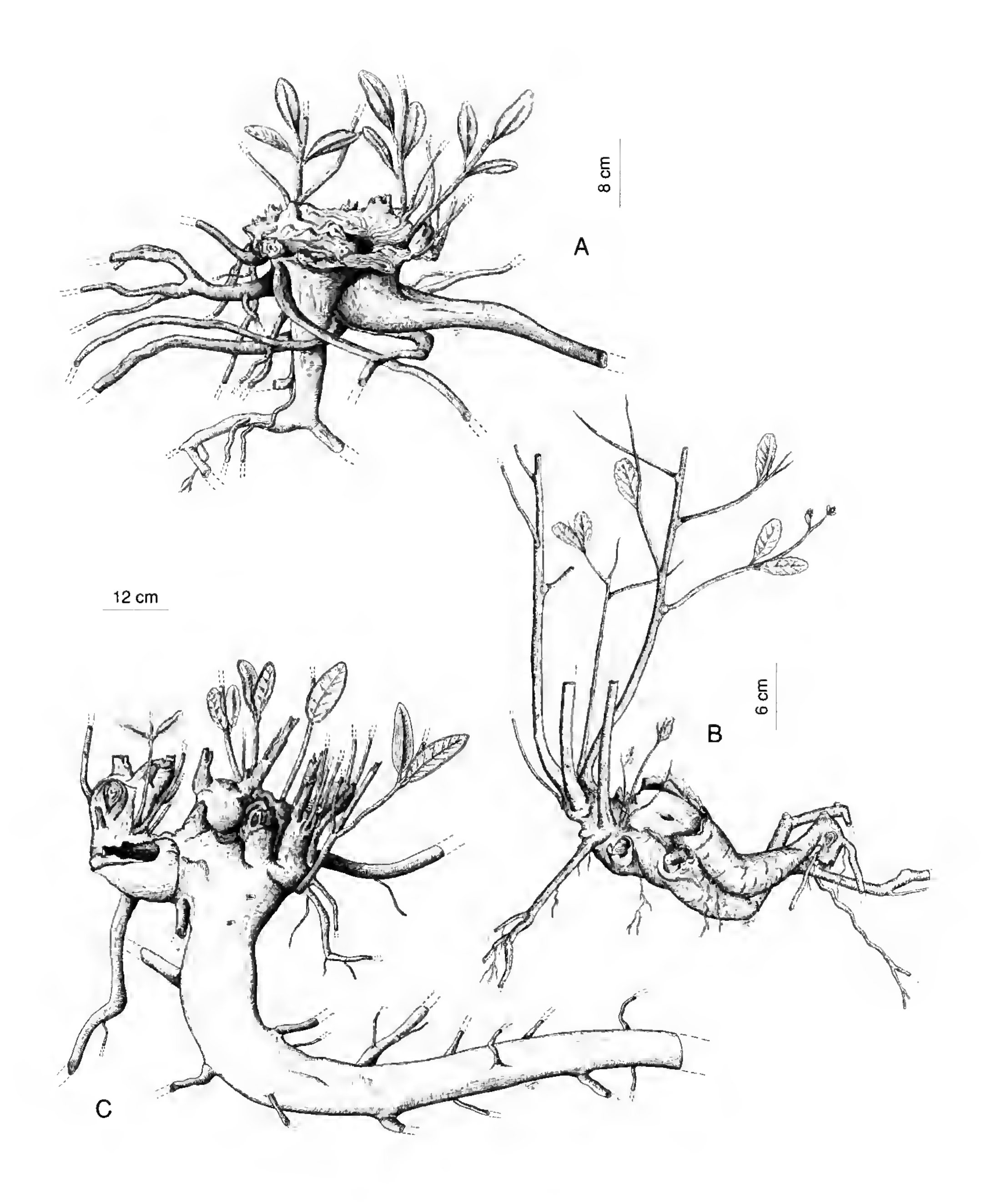


Fig. 8. — Exemples de bourrelets ligneux (lignotuber) chez quelques espèces du maquis ligno-herbacé sur roches ultramafiques : **A**, ***Tristaniopsis glauca*** ; **B**, ***Peripterygia marginata*** ; **C**, ***Garcinia amplexicaulis***.

qui germent dès les premières pluies après l'incendie. Les autres espèces, comprenant toutes les Epacridaceae, ne se réinstallent que plus tard par apports successifs de semences.

La majorité des espèces des maquis ligno-herbacés résistent au feu, bien que la partie aérienne soit entièrement détruite. C'est le cas parmi les espèces herbacées, des Orchidaceae, *Megastylis gigas* et *Eriaxis rigida*, qui fleurissent abondamment dès les premières pluies suivant l'incendie, ainsi que celui des espèces rhizomateuses, *Pteridium esculentum*, *Schizaea spp.* (fougères), *Lepidosperma perteres* (Cyperaceae), *Dianella stipitata* (Liliaceae). C'est aussi le cas de la majorité des espèces arbustives qui, après l'incendie, développent des rejets à croissance rapide, à partir de bourrelets ligneux (lignotuber) situés au niveau du collet (Fig. 7, 8). Elles appartiennent à des familles variées (Myrtaceae, Cunoniaceae, Dilleniaceae) dont les espèces sont souvent dominantes dans la strate arbustive des maquis miniers.

Ces bourrelets ligneux et robustes peuvent atteindre jusqu'à 1 m de diamètre pour certains *Tristaniopsis spp.* (Myrtaceae), témoignant de la longévité de ces espèces et de l'ancienneté des incendies répétés.

Quelques espèces, dont *Guioa villosa* (Sapindaceae) et *Montrouziera sphaeroidea* (Guttiferae) émettent des rejets de racines après l'incendie. Parmi les espèces ligneuses résistantes au feu, une seule, *Babingtonia leratii* (Myrtaceae) se régénère dès la première année suivant l'incendie, simultanément à partir de rejets et de germinations.

DISCUSSION ET CONCLUSION

Au stade actuel des observations, on constate que l'effet de l'incendie se manifeste de manière sensiblement identique sur les deux catégories de maquis ligno-herbacés. Les seules différences étant le développement plus important de la strate arbustive sur haut versant que sur piémont, l'inverse s'observant pour la strate des Cyperaceae cespiteuses.

Les suivis réalisés sur ces deux stations pendant plus de 10 ans, complétés par plusieurs autres observations sur les maquis ligno-herbacés du même secteur géographique, permettent de faire un certain nombre de commentaires et de tirer quelques conclusions.

Les modifications de la composition floristique provoquées par l'incendie sont peu importantes et ne semblent pas définitives. En effet, les quelques espèces qui ne sont pas réapparues, demeurent largement représentées dans des maquis voisins n'ayant pas brûlé depuis au moins 30 années. En outre, parmi les espèces supplémentaires, *Baumea deplanchei*, dont la présence demeure discrète dans les deux cas étudiés, et qui est absente des maquis plus anciens, ne s'installe manifestement pas de manière durable. Par contre, *Pinus caribaea* qui s'implante volontiers sur les piémonts, peut s'y maintenir et sans doute, à plus long terme, s'y multiplier. On n'a pas encore pour cette espèce (introduite dans les années soixante) suffisamment de recul pour tirer des conclusions définitives sur le rôle du feu dans sa prolifération.

D'une manière générale, l'effet de l'incendie se traduit principalement par un changement de la structure du maquis, engendré par la modification de l'abondance relative des principales composantes de la flore. Ainsi assiste-t-on au remplacement de la strate cypéracéenne cespiteuse par une strate cypéracéenne jonciforme. Ce changement s'accompagne du développement, variable suivant les sites, de *Pteridium esculentum*, qui toutefois périclite progressivement dans les conditions habituelles, comme cela a été montré dans les deux stations étudiées. L'incendie a aussi pour effet de détruire la totalité de la biomasse ligneuse aérienne et par contrecoup, d'induire l'émission de jeunes pousses chez la plupart des espèces arbustives, sauf chez quelques-unes appartenant notamment aux familles des Epacridaceae et des Araliaceae. Ces dernières se réinstalleront toutefois progressivement à partir de semences. Aussi, malgré une émission rapide de rejets, la strate arbustive mettra plus de 10 années pour se reconstituer.

La strate cypéracéenne cespiteuse, qui constitue un matériel végétal très inflammable en saison sèche, ne se réinstalle que très lentement à partir de semences et laisse place à une strate cypéracéenne jonciforme ininflammable qui met le

maquis à l'abri des feux pendant plusieurs années. Ceci à condition toutefois qu'un développement trop important de *Pteridium esculentum* n'entraîne pas une accumulation de frondes sèches, propice à la propagation des incendies.

La succession secondaire après incendie des maquis ligno-herbacés, qui se limite donc à un phénomène de retour au stade initial, sans passage par des stades successifs intermédiaires, floristiquement différenciés, est très largement déterminée par la composition floristique avant l'incendie. Le phénomène s'apparente donc au modèle de la composition initiale proposé par EGLER (1954).

Ce phénomène, qui se caractérise finalement par l'absence de changement de la composition floristique est assez général ; il a été décrit dans le Bassin Méditerranéen (TRABAUT 1987 ; CODY & MOONEY 1976), en Australie (RUSSELL & PARSON 1978 ; SPECHT, RAYSON & JACKMAN 1958), en Afrique du Sud (VAN WILGEN 1981 ; VAN WILGEN & KRUGER 1981 ; GILL & GROVES 1984), en Floride (ABRAHAMSON 1984 ; GIVENS et al. 1984), en Californie (HANES 1970 ; MALANSON 1984) et concerne aussi bien des maquis, des garrigues, le chaparral, des landes (heathlands), des formations herbeuses ou des formations dominées par des pins. Il a été qualifié « d'autosuccession » par plusieurs des auteurs précédemment cités.

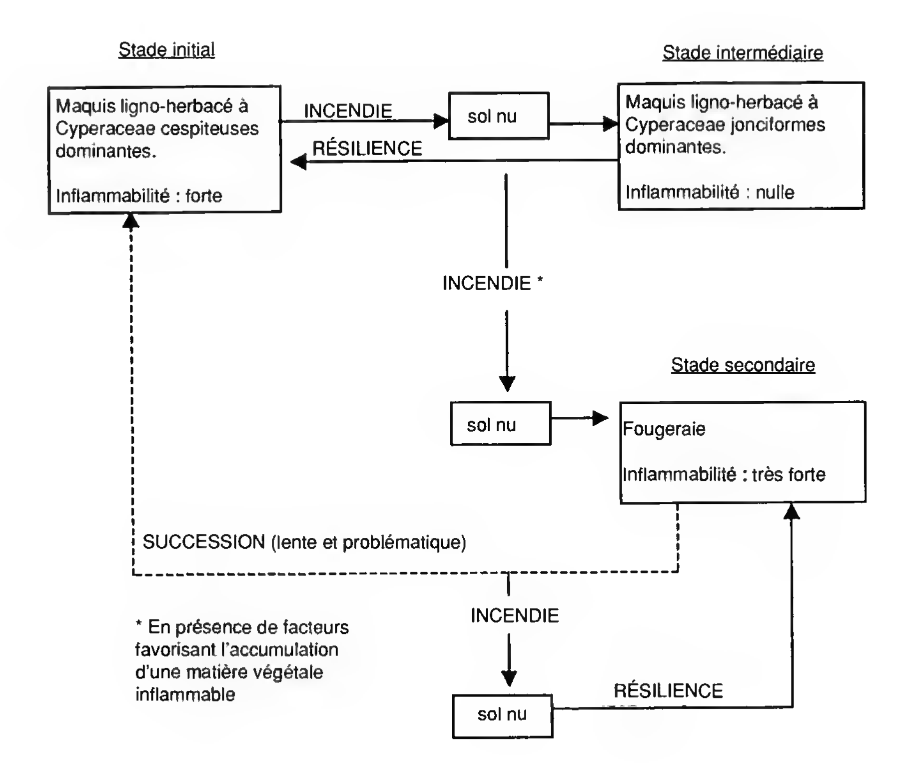


Fig. 9. — Représentation des différentes phases de l'évolution post-incendie des maquis ligno-herbacés.

Il apparaît ainsi que le maquis ligno-herbacé des terrains miniers de Nouvelle-Calédonie est une formation secondaire adaptée aux incendies. Il peut être qualifié de « maquis pyrophyte », sa destruction par le feu étant suivie par un phénomène de reconstitution, lent en raison des conditions édaphiques, mais sans changement profond du type de végétation ni de la flore. Il s'agit donc d'un processus de résilience, au sens de HOLLING (1973), qui traduit la capacité du système écologique à répondre à une perturbation par le retour au stade ayant précédé celle-ci.

Le processus étudié correspond au schéma le plus commun. Il y a lieu cependant de souligner que, parfois, de nouveaux incendies interviennent au cours des premières phases de la reconstitution. C'est notamment le cas lorsque la présence de *Pinus caribaea* entraîne localement, sous son couvert, l'accumulation d'une litière très inflammable en saison sèche. Celle-ci est formée d'aiguilles de pins et de frondes desséchées de *Pteridium esculentum* qui prolifère naturellement sous les pins. L'incendie qui survient alors entraîne la disparition de certaines composantes les plus sensibles de la flore. C'est le cas notamment de ligneux qui n'ont pas le temps nécessaire pour accumuler les réserves leur permettant de rejeter rapidement de souche, et celui des espèces qui doivent fructifier pour régénérer le potentiel séminal. Ces disparitions se font toujours au profit de *Pteridium esculentum* qui devient l'espèce dominante. On est alors en présence d'une fougeraie qui apparaît comme le stade ultime de la dégradation par le feu sur sols ferrallitiques ferritiques moyennement à fortement désaturés sur substrat d'origine ultramafique. Ce stade, une fois installé, « s'auto-entretient » en raison de la forte inflammabilité des frondes sèches produites chaque année.

Ces différentes phases de l'évolution post-incendie des maquis ligno-herbacés sont schématisées Figure 9.

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Callistemon of New Caledonia transferred to *Melaleuca* (Myrtaceae)

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KEY WORDS
Myrtaceae,
Callistemon,
Melaleuca,
New Caledonia.

ABSTRACT
The endemic New Caledonian taxa of *Callistemon* (five species and one nonautonymic variety) are transferred to *Melaleuca*. An identification key for the New Caledonian taxa of *Melaleuca* is presented.

MOTS CLÉS
Myrtaceae,
Callistemon,
Melaleuca,
Nouvelle-Calédonie.

RÉSUMÉ
Les cinq espèces de *Callistemon* endémiques de Nouvelle-Calédonie sont transférées dans le genre *Melaleuca*. Une clé des *Melaleuca* néo-calédoniens est proposée.

Callistemon R. Br. conventionally has been separated from *Melaleuca* L. on the basis of the former genus having the stamens dispersed around the hypanthium apex and free staminal filaments whereas in *Melaleuca* the stamens are in five groups opposite the petals and the filaments within each group fused proximally for part, sometimes the greater part, of their length. The occurrence of 5-grouped, fused stamens in *Callistemon* has been long known, e.g. BENTHAM (1867) recorded this condition in the Western Australian *C. glaucus* (Bonpl.) Sweet (as *C. speciosus* DC.). More recently, BYRNES (1984) transferred the eastern Australian *C. viminalis* (Sol. ex Gaertner) G. Don ex Loudon to *Melaleuca* on the basis that this species has its stamens in bundles (i.e. 5-grouped and fused).

Eight species of the *Melaleuca-Callistemon* complex occur in New Caledonia (DAWSON 1992) with seven of them endemic and, of the five species attributed to *Callistemon*, two have the stamens in bundles, i.e. *C. buseanus* Guillaumin and *C. gnidioides* Guillaumin (the latter variably so, the stamens ranging from free to 5-grouped and fused). In addition, adjacent stamens occasionally may be fused at the filament base in *C. brevisepalus* J.W. Dawson and *C. suberosus* Pancher ex Brongn. & Gris. Due to their many shared features, DAWSON (1978) previously had given a combined generic description of *Melaleuca* and *Callistemon* in New Caledonia.

In view of the morphological similarities between the endemic New Caledonian species of the complex there is no doubt that these belong to the same genus. They may well be related to some of the eastern Australian species of *Melaleuca*, notably to *M. styphelioides* Sm. and its closer relatives; these species in particular have quite similar leaves to several of the New Caledonian species. The Australian species of *Callistemon* are not especially closely related to the New Caledonian taxa and are presently being studied by L.A.C. as part of a broader project dealing with *Melaleuca*. The New Caledonian group of species, in our opinion, fits comfortably within *Melaleuca* and the necessary transfers of the six taxa currently ascribed to *Callistemon* are effected below.

The non-endemic New Caledonian species, *Melaleuca quinquenervia* (Cav.) S.T. Blake, occurs in New Guinea and Australia also (BLAKE 1968; CRAVEN in press); it is a member of the broad-leaved group of paperbarks centred upon *M. leucadendra* (L.) L., the type species of *Melaleuca*.

Melaleuca dawsonii Craven, **nom. nov.**

Callistemon suberosum Pancher ex Brongn. & Gris, Bull. Soc. Bot. France 11: 183 (1864).—Lectotype: *Pancher s.n.*, 1861 (P!), designated by DAWSON, Fl. Nouvelle-Calédonie et dépendances 18: 230 (1992).

Unfortunately, the specific epithet "*suberosa*" is pre-empred in *Melaleuca* by *M. suberosa* (Schauer) C.A. Gardner and a new epithet is required in that genus. The new epithet provided above honours John Wyndham DAWSON, who has researched New Caledonian Myrtaceae for many years and co-authors this contribution.

Melaleuca pancheri (Brongn. & Gris) Craven & J.W. Dawson, **comb. nov.**

Callistemon pancheri Brongn. & Gris, Bull. Soc. Bot. France 11: 183 (1864).—Lectotype: *Deplanche 513* (P!), designated by DAWSON, Fl. Nouvelle-Calédonie et dépendances 18: 234 (1992).
Callistemon suberosum var. *microphyllum* Guillaumin, Mém. Mus. Natl. Hist. Nat. Paris 8: 277 (1962).—Type: *Hürlimann 1389* (holo-, P!).

Melaleuca buseana (Guillaumin) Craven & J.W. Dawson, **comb. nov.**

Callistemon buseanum Guillaumin, Bull. Mus. Natl. Hist. Nat. 11: 414 (1939).—Type: *Virot s.n.* (holo-, P!).
Callistemon buseanum var. *longifolium* Guillaumin, Mém. Mus. Natl. Hist. Nat. Paris 8: 276 (1962), *nom. inval.* (Type not designated).

Melaleuca sphaerodendra Craven & J.W. Dawson, **nom. nov.**

Callistemon gnidioides Guillaumin, Bull. Soc. Bot. France 81: 6, 12 (1934).—Type: *Cribs 1213* (holo-, P!).

A new specific epithet is required as "*gnidioides*" is pre-empted in *Melaleuca* by *M. gnidioides* Brongn. & Gris. The epithet selected is derived from the Greek *sphaera* (ball, sphere) and *dendron* (tree) in reference to the shape of the crown in many plants of this species. Two varieties are distinguished:

Melaleuca sphaerodendra var. **sphaerodendra**

Melaleuca sphaerodendra var. **microphylla** (Virot) Craven & J.W. Dawson, **comb. nov.**

Callistemon gnidioides var. *microphyllum* Virot, Mém. Mus. Natl. Hist. Nat., ser. B, Bot. 4: 30 (1953).—Type: *Virot 1313* (holo-, P!).

Melaleuca brevisepala (J.W. Dawson) Craven & J.W. Dawson, **comb. nov.**

Callistemon brevisepalus J.W. Dawson, Fl. Nouvelle-Calédonie et dépendances 18: 242 (1992).—Type: *MacKee 39344* (holo-, P!).

Key to the New Caledonian species of *Melaleuca*

1. Leaves 8 mm or more wide 2
1'. Leaves 6 mm wide or less 4
2. Inflorescences spicate, the groups of flowers or capsules separated by well-marked internodes .... **M. quinquenervia**
2'. Inflorescences capitate, the flowers or capsules densely aggregated and not separated by well-marked internodes 3
3. Leafy twigs 8-11 mm in diameter .... **M. dawsonii**
3'. Leafy twigs 2.5-3.5 mm in diameter .... **M. pancheri**
4. Inflorescences spicate, the groups of flowers or capsules separated by well-marked internodes .... **M. buseana**
4'. Inflorescences capitate, the flowers or capsules densely aggregared and nor separared by well-marked internodes 5
5. Stamens 25 or more per flower, fused at the base in 5 groups. (Shrubs in the far south, mostly in stream beds or swamps) 6
5'. Stamens 12 or fewer per flower, free or slightly fused at the base in 5 groups. (Shrubs to small trees with dense rounded crowns, on well-drained slopes in the north and south) 7
6. Leaves with evident parallel veins .... **M. gnidioides**
6'. Leaves with obscure parallel veins .... **M. brongniartii**
7. Stamens longer than the style, capsule glabrous 8
7'. Stamens shorter than the style, capsule densely pubescent .... **M. brevisepala**
8. Leaves 3.5-5 mm wide .... **M. sphaerodendra var. sphaerodendra**
8'. Leaves 2-3 mm wide .... **M. sphaerodendra var. microphylla**

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Architecture de l'appareil végétatif et organisation florale du *Dracontium polyphyllum* L. (Araceae)

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MOTS CLÉS
Dracontium,
Araceae,
fleur,
architecture,
inflorescence,
développement.

RÉSUMÉ
Une description de l'appareil végétatif, du développement de la feuille et de l'anatomie florale du *Dracontium polyphyllum* est présentée dans le cadre d'une analyse comparative avec les genres *Anchomanes* et *Amorphophallus*. Du point de vue architectural, le *D. polyphyllum* peut être classé dans trois catégories différentes selon le cadre théorique adopté. Si l'on adopte la classification d'ENGLER (1877), cette espèce fait partie du type V de la septième série qui comprend plusieurs espèces à tubercules. D'autre part, si l'on adopte la classification architecturale d'HALLÉ & OLDEMAN (1970), le *D. polyphyllum* correspond au modèle de Chamberlain. Finalement, si l'on suit la classification de RAY (1987), cette espèce aurait une organisation de type anisophylle proleptique. La lobation foliaire a un mode de développement marginal et intramarginal. Dans l'inflorescence, la maturation des fleurs est basipète. La fleur comprend trois ou quatre carpelles et généralement de 9 à 12 étamines.

KEY WORDS
Dracontium,
Araceae,
flower,
architecture,
inflorescence,
development.

ABSTRACT
A description of the vegetative architecture, the development of the leaf and the floral anatomy of *Dracontium polyphyllum* is presented in comparison with the genera *Anchomanes* and *Amorphophallus*. From an architectural point of view, *D. polyphyllum* can be put in three different categories depending on the theoretical framework chosen. If we use the classification of ENGLER (1877), this species belongs to the type V of the seventh series, which comprises many tuberous species. On the other hand, if we adopt the architectural classification of HALLÉ & OLDEMAN (1970), *D. polyphyllum* corresponds to Chamberlain's model. Finally, if we follow RAY's classification (1987) this species would have an organisation of the proleptic anisophyllous type. The foliar lobation has a marginal and intramarginal mode of development. The flower maturation in the inflorescence is basipetal. The flower comprises three or four carpels and generally 9 to 12 stamens.

INTRODUCTION

Les Araceae comptent plus de 100 genres et 3000 espèces présentant différents types de croissance, tels que lianescents, épiphytiques aquatiques ou géophytiques (HAY & MABBERLEY 1991). Parmi les géophytes, on trouve, entre autres, les genres *Dracontium* avec 23 espèces néotropicales (ZHU & GRAYUM 1995), *Anchomanes* avec 10 espèces africaines et *Amorphophallus* avec 100 espèces paléotropicales (GRAYUM 1990).

En général, les espèces de ces genres ne produisent annuellement qu'une seule inflorescence et une seule feuille très découpée, pouvant atteindre jusqu'à 5 m de longueur chez l'*Amorphophallus titanum* (GANDAWIJAJA et al. 1983). ENGLER (1911) plaçait ces trois genres dans la même sous-famille, les Lasioideae. Par contre, GRAYUM (1990) les classe dans trois sous-familles différentes ; le genre *Dracontium* dans les Lasioideae, le genre *Amorphophallus* dans les Aroideae et le genre *Anchomanes* dans les Philodendroideae.

Le mode de croissance des géophytes tropicales en fait un matériel de choix pour l'étude de l'architecture des plantes herbacées, qui demeure toujours un domaine peu connu de la morphologie, l'architecture de l'appareil végétatif ayant surtout été analysée chez les arbres (CORNER 1952 ; HALLÉ & OLDEMAN 1970 ; HALLÉ et al. 1978 ; TOMLINSON 1962). Rappelons cependant que les 24 modèles architecturaux décrits par HALLÉ & OLDEMAN ont été repris dans des travaux concernant l'architecture des sous-arbustes, des plantes herbacées et des lianes (BLANC 1978 ; CREMERS 1973, 1974, 1977, 1986, 1992 ; CREMERS & SELL 1986 ; JEANNODA-ROBINSON 1977 ; N'DIAYE 1977 ; POISSON 1996). ENGLER (1877) et plus récemment RITTERBUSCH (1971), BLANC (1977a,b, 1978, 1980), RAY (1987b, 1988) et HAY (1992) se sont intéressés à l'organisation de l'appareil végétatif des Araceae sans approfondir pour autant la question des espèces géophytiques. Dans cette optique, l'analyse détaillée de l'organisation végétative et du mode de croissance du *Dracontium polyphyllum* amènera une meilleure compréhension de l'architecture des plantes géophytiques en général et celle des Araceae en particulier.

Différents auteurs ont décrit sommairement l'organisation de l'appareil végétatif du *Dracontium polyphyllum* (ENGLER 1877, 1911 ; HAY & MABBERLEY 1991 ; HAY 1992 ; ZHU & GRAYUM 1995). Néanmoins, ces études se fondent sur l'analyse d'un ou deux spécimens et ne tiennent pas compte de la variabilité qui peut exister entre individus. L'observation de plusieurs spécimens nous permettra de montrer la variabilité intraspécifique et de faire ressortir les modes de croissance les plus fréquents.

Cette étude comprend aussi des observations sur l'anatomie de l'appareil reproducteur. Plusieurs travaux ont été publiés sur l'organisation florale des Araceae (e.g. EYDE et al. 1967 ; HOTTA 1971 ; BARABÉ & FORGET 1992 ; LEHMANN & SATTLER 1992 ; SCRIBAILO & TOMLINSON 1992 ; BARABÉ & BERTRAND 1996 ; BOUBES & BARABÉ 1997). Cependant aucun d'eux ne traite de façon détaillée de l'anatomie florale des *Dracontium*. Afin de combler cette lacune, il nous a semblé approprié d'inclure quelques observations sur l'organisation florale du *D. polyphyllum*, même si celles-ci ne font pas l'objet d'une analyse comparative détaillée. Ces observations pourront servir dans des études plus générales portant sur l'ensemble de la famille.

Le présent article a donc pour principal objectif l'analyse de l'architecture de l'appareil végétatif du *D. polyphyllum* en relation avec celle des genres *Amorphophallus* et *Anchomanes*. Cette analyse s'accompagne d'une description des organes végétatifs et reproducteurs.

MATÉRIEL ET MÉTHODES

Les spécimens de *Dracontium polyphyllum* utilisés dans cette étude ont été récoltés en Guyane française, dans la région des montagnes de Kaw, au sud-est de Cayenne, en mai 1994 et en 1995. Lors de la récolte, les échantillons ont été fixés au F.A.A. (90 ml d'éthanol 70%, 5 ml de formol du commerce à 35% et 5 ml d'acide acétique).

Microscopie électronique. — Les inflorescences et les primordiums foliaires ont été observés à l'aide du microscope électronique à balayage (MEB) JEOL JMS35 du Département de sciences biologiques de l'Université de Montréal.

Les échantillons choisis ont été préalablement déshydratés suivant une série ascendante d'éthanol, séchés au point critique avec du CO_2 liquide dans une bombe Polaron, montés sur supports métalliques et métallisés à l'or-palladium. Les observations ont été réalisées à des kilovoltages différents selon les échantillons (15kV à 25kV).

Microscopie optique. — Pour la microscopie optique, des inflorescences à différents stades de développement furent déshydratées suivant une série ascendante de butanol. Pour faciliter l'orientation des petits spécimens, nous les avons colorés à l'érythrosine alcoolique en cours de déshydratation. Cette étape fut suivie d'un enrobage dans la paraffine selon la technique habituelle (GURR 1956). Les coupes sériées (10 µm) d'inflorescences ont été colorées à la safranine 1% (diluée dans de l'eau distillée) et au bleu d'aniline 1% (dilué dans de l'éthanol 100%). Les photomicrographies des coupes furent prises à l'aide de l'Axiomat Zeiss du Département de sciences biologiques de l'Université de Montréal.

Diagrammes de l'architecture de l'appareil végétatif. — Les diagrammes de l'architecture de l'appareil végétatif des spécimens juvéniles ont été tracés à partir de la dissection de 8 bulbilles rapportées de la Guyane française en 1994 et mises en culture dans les serres du Jardin Botanique de Montréal. Quant aux spécimens adultes, les diagrammes de l'architecture de l'appareil végétatif ont été réalisés à partir de trois sources. Sur les 51 plants récoltés, 41 furent disséqués sur le terrain lors de la récolte, 11 en 1994 et 30 en 1995. Des 10 plants rapportés et conservés en serre au Jardin Botanique de Montréal, 5 furent disséqués et servirent de modèle pour dessiner les diagrammes. Finalement, un plant conservé dans une mini-serre à température, humidité et luminosité contrôlées, fut observé quotidiennement de la floraison à l'apparition de la feuille annuelle.

RÉSULTATS ET DISCUSSION

DESCRIPTION DES APPAREILS VÉGÉTATIF ET REPRODUCTEUR

Tige. — Le tubercule, à face supérieure concave et à face inférieure convexe, est entouré de

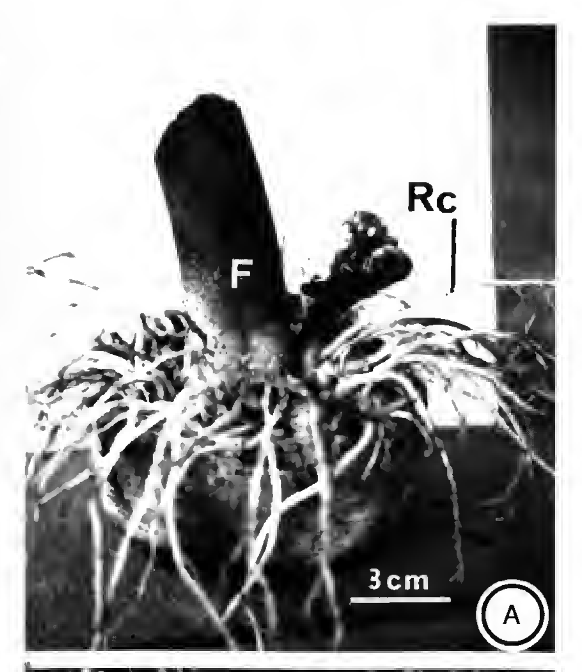




Fig. 1. — ***Dracontium polyphyllum*** : **A**, tubercule (F, base du pétiole ; Rc, racine contractile) ; **B**, feuille.

racines contractiles sur sa face supérieure (Fig. 1A). Il peut atteindre 30 cm de diamètre et 20 cm de hauteur chez des spécimens ayant une feuille de près de 2 m. Lors de la sénescence de la feuille (Fig. 1B), on peut distinguer au sommet du tubercule le bourgeon apical (Fig. 2A). La propagation de la plante peut aussi s'effectuer à l'aide des bulbilles présentes à la face supérieure du tubercule. Les bulbilles donneront des plantes à croissance monopodiale.

Feuille. — La feuille composée, en forme de parasol, comprend un limbe fortement divisé, soutenu par un long pétiole marbré de violet (Fig. 1B). Son limbe est divisé en trois rachis primaires de dimension égale (Fig. 2B). Généralement d'une longueur de 1 m, le pétiole peut parfois atteindre plus de 2 m. La nervation du limbe paraît réticulée, semblable à celle des Dicotylédones, comme chez la plupart des Lasioideae. En règle générale, plusieurs cataphylles précèdent la feuille unique produite annuellement ; cependant, chez environ 10% des spécimens observés, on note la présence de deux feuilles. Chez les individus portant deux feuilles, la deuxième occupe la position de la première cataphylle et appartient donc au même article (Fig. 8F).

Inflorescence. — Le spadice de 4-7 cm de longueur et de 1-3 cm de largeur est entouré par une spathe de 7-15 cm de longueur et de 2-8 cm de largeur, dont la surface interne est mauve-violet (Fig. 3A). La spathe, qui se recourbe selon un angle de 45° à l'apex, ne couvre pas entièrement le spadice, bien que les marges se chevauchent (Fig. 3B). L'inflorescence est portée par un pédoncule de 2 à 15 cm de longueur (ces mesures incluent la portion souterraine) et de 0,5 à 2 cm de largeur. Nous avons dénombré de 150 à 290 fleurs par inflorescence. À la base de celle-ci se trouve une cataphylle qui est souvent plus longue que le pédoncule. Comme pour les Lasieae en général, la maturation des fleurs sur l'inflorescence se fait de façon basipète (Fig. 4A). Soulignons que ce type de maturation est contraire à ce qui a été observé chez d'autres Araceae (BARABÉ 1994).

Fleur. — La fleur hypogyne se compose de 5, 6 (90% des spécimens observés) ou 7 tépales, généralement de 9-12 étamines, quelquefois 7, dispo-



Fig. 2. — ***Dracontium polyphyllum*** : **A**, bourgeon apical au sommet du tubercule (E, cataphylle) ; **B**, limbe de la feuille divisé en trois rachis primaires.

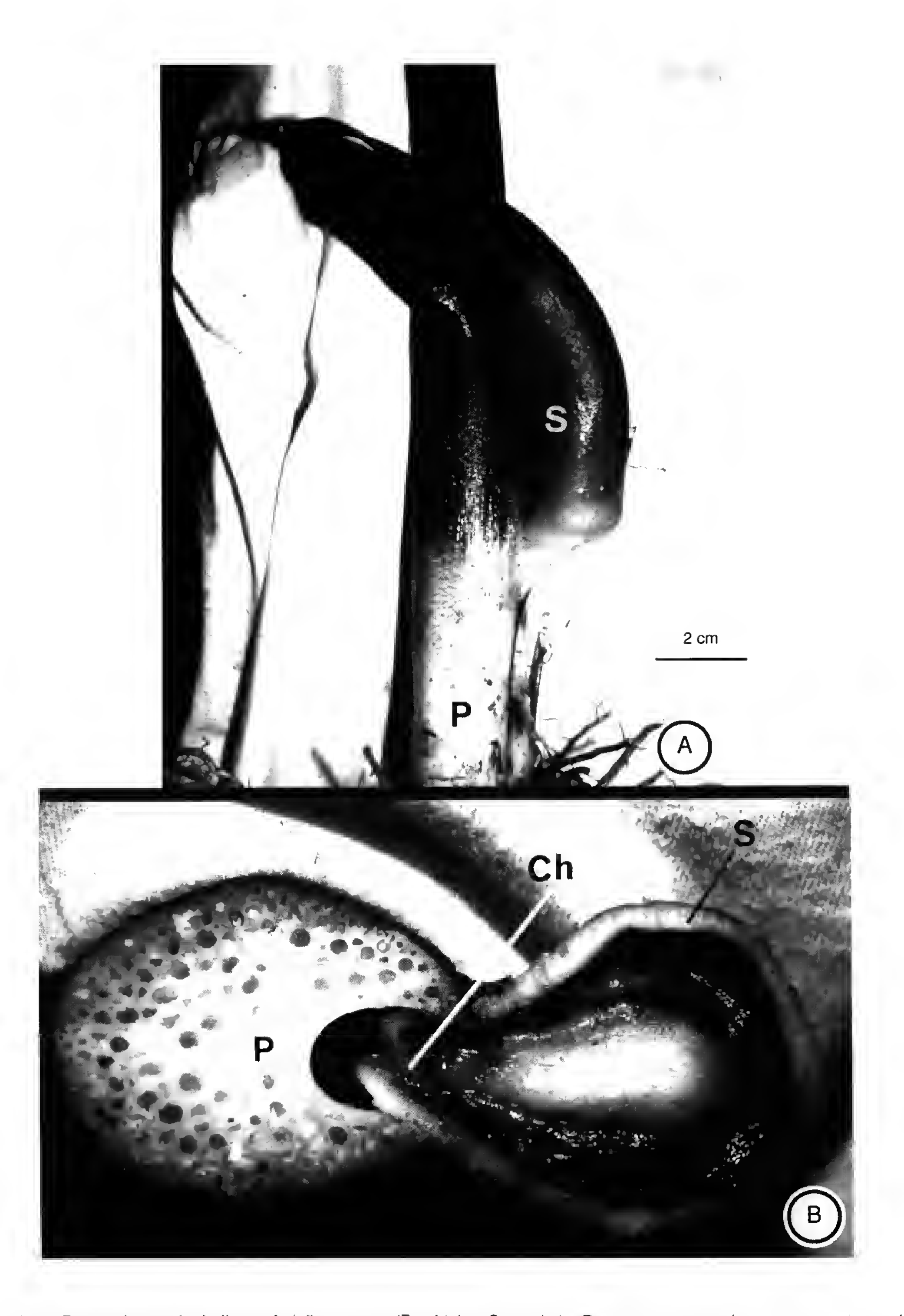


Fig. 3. — ***Dracontium polyphyllum*** : **A**, inflorescence (P, pétiole ; S, spathe) ; **B**, coupe transversale passant au niveau de la spathe du spécimen de la figure A (Ch, chevauchement des marges de la spathe ; S, spathe ; P, pétiole).

sées sur deux verticilles, et d'un gynécée triloculaire (90% des spécimens observés) ou tétraloculaire (Fig. 4B-C). Chaque loge renferme un ovule inséré en position axile, dans la partie médiane de l'ovaire. Il ne semble pas y avoir de règle concernant la position des gynécées tétraloculaires sur l'inflorescence ; ils sont dispersés au hasard parmi les fleurs à gynécées triloculaires. La déhiscence des étamines, confinée à la partie supérieure de l'anthère, est longitudinale. Des coupes transversales de la partie supérieure de l'ovaire supère montrent que chaque carpelle

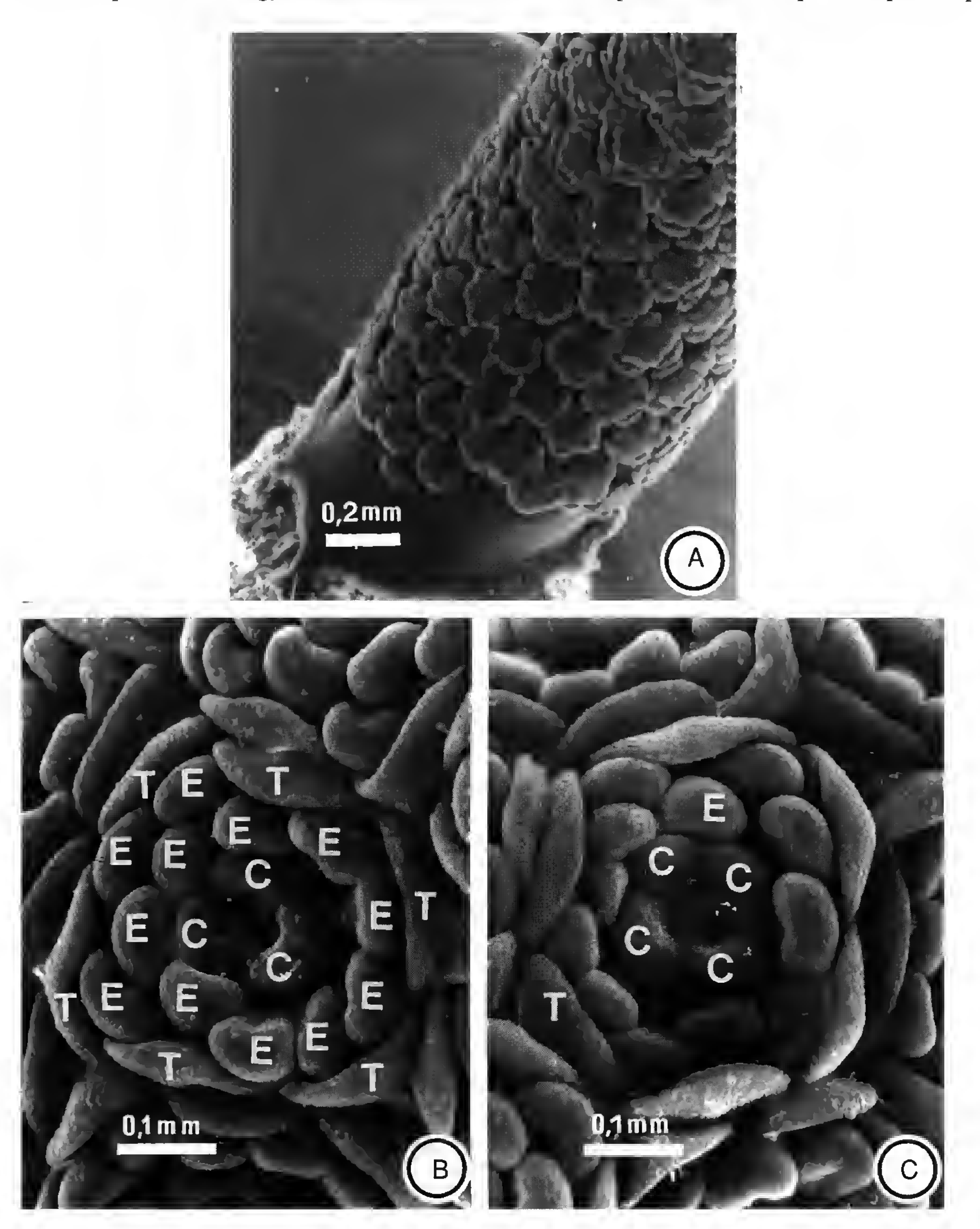


Fig. 4. — ***Dracontium polyphyllum*** : **A**, portion d'inflorescence montrant la maturation basipète des fleurs ; **B**, fleur à gynécée triloculaire ; **C**, fleur à gynécée tétraloculaire. (E, étamine ; C, carpelle ; T, tépale).

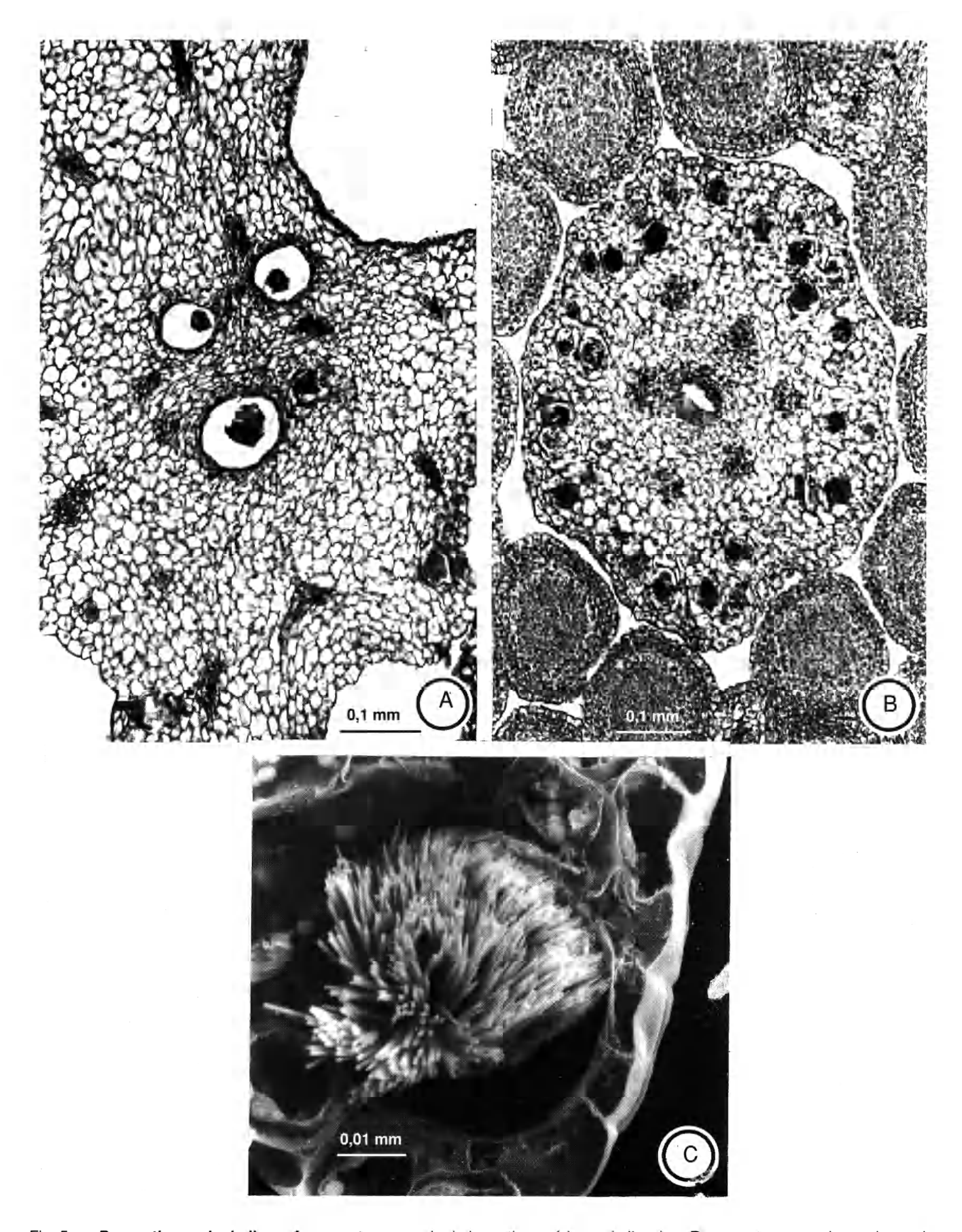


Fig. 5. — ***Dracontium polyphyllum*** : **A**, coupe transversale de la partie supérieure de l'ovaire ; **B**, coupe transversale au niveau du style ; les canaux stylaires se fusionnent en un seul ; **C**, coupe transversale d'un tépale montrant un idioblaste à raphides d'oxalate de calcium.

possède un canal stylaire qui lui est propre. Toutefois, dans le style, les canaux se fusionnent en un seul (Fig. 5A-B). Les pièces florales du *D. polyphyllum* se développent dans un sens acropète (Fig. 4A) : d'abord les tépales, suivis des étamines et du gynécée. Durant le développement, les tépales recouvrent progressivement le reste de la fleur. Contrairement à la plupart des Araceae, le style du *D. polyphyllum* est plutôt long. Toutes les pièces florales renferment des idioblastes à raphides d'oxalate de calcium, comme c'est généralement le cas chez les Araceae (Fig. 5C).

Fruit. — La baie de forme obpyramidale mesure environ 2 cm de longueur et 2 cm de largeur

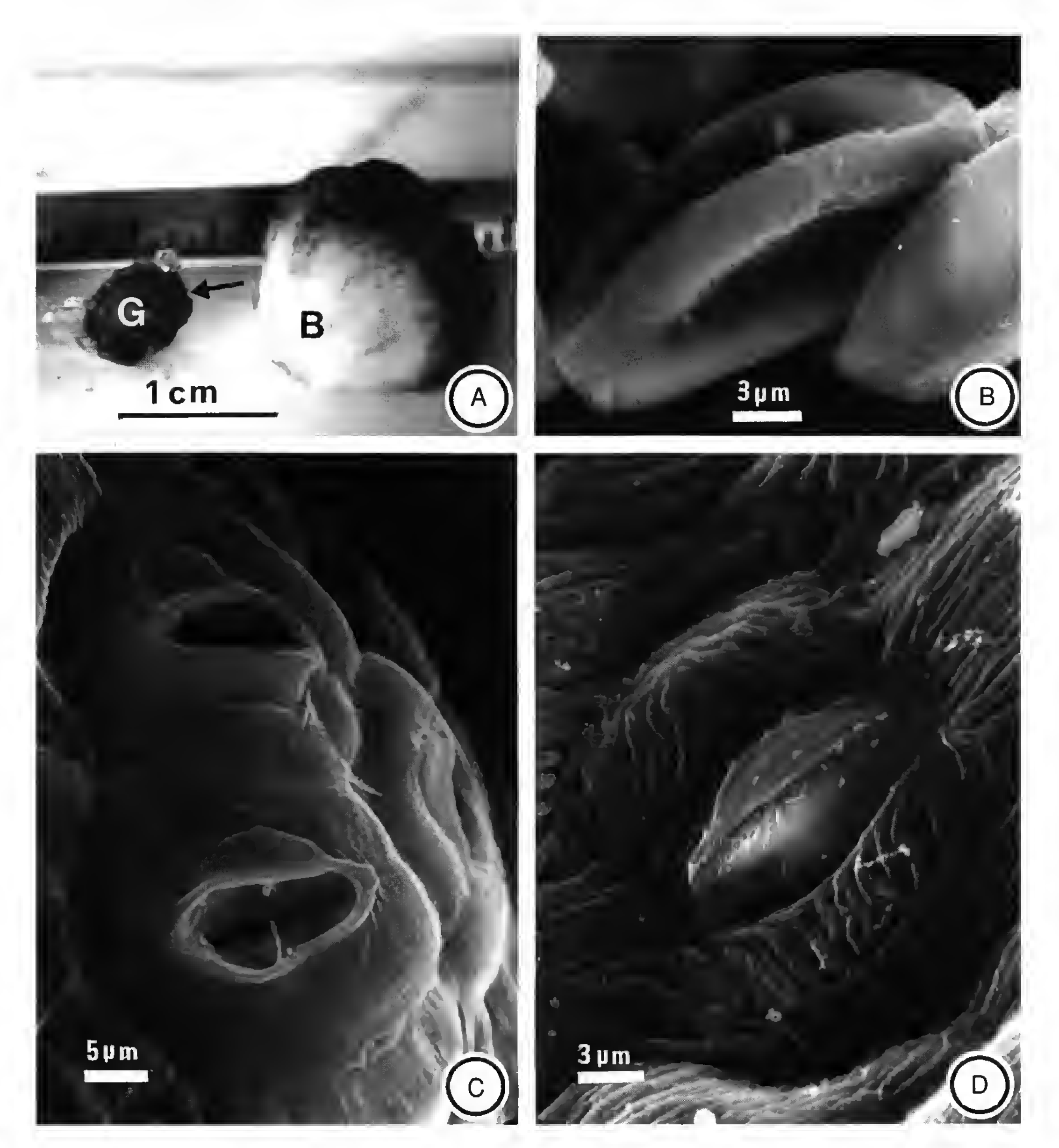


Fig. 6. — ***Dracontium polyphyllum*** : **A**, graine (G) et fruit (baie) (**B**), la flèche indique les excroissances ; **B**, pollen monocolpé ; **C**, groupe de trois stomates dans la partie supérieure de l'inflorescence ; **D**, stomate diacytique sur le gynécée.

(Fig. 6A) ; le péricarpe plus ou moins dur est vert foncé. Chaque fruit renferme trois à quatre graines entourées de mucus.

Graine. — La graine albuminée du *D. polyphyllum* est téniforme comme toutes celles des genres de Lasieae (SEUBERT 1993). Elle arbore un testa dur de couleur brun-noir, muni de petites excroissances sur le contour de la partie supérieure (Fig. 6A, flèche). Elle est convexe sur les deux côtés et mesure environ 9 mm de largeur, 7 mm de hauteur et 4 mm d'épaisseur.

Pollen. — Le pollen monocolpé de grandeur moyenne (34 µm), possède une exine réticulée. Il a une forme de bateau elliptique à symétrie bilatérale (Fig. 6B). L'aperture est située au pôle distal comme chez les Monocotylédones en général (GRAYUM 1992 ; REILLE 1990).

Stomates. — Des stomates de type cyclocytique ont été observés entre les primordiums floraux. Au sommet de l'inflorescence se trouvent souvent des groupes de trois ou quatre stomates (Fig. 6C). Les stomates de la surface inférieure des feuilles sont paracytiques, tandis que ceux présents sur le gynécée sont diacytiques selon la classification de METCALFE & CHALK (1979) (Fig. 6D).

CROISSANCE ET ARCHITECTURE

Tubercule. — Le *D. polyphyllum* forme généralement des tubercules orthotropes qui, à la rencontre d'un obstacle, peuvent devenir pseudo-rhizomateux, plagiotropes. Ceci diffère de ce qui a été rapporté par KNECHT (1983) pour le genre *Anchomanes*. Les espèces de ce genre produisent un tubercule plagiotrope, où un nouveau tubercule, issu d'un bourgeon latéral provenant de l'axe principal apparaît annuellement sans que celui de l'année antérieure ne meure. La croissance du tubercule de *D. polyphyllum* est monopodiale jusqu'à la maturité sexuelle ; par la suite, il adopte un mode de croissance sympodial (ENGLER 1877).

Cataphylle. — Comme chez la plupart des Araceae, l'initiation d'un nouvel axe chez le *D. polyphyllum* est associée à la présence de feuilles spécialisées, les cataphylles ; le limbe est rudimentaire ou même quelquefois absent. Les premiers stades du développement des cataphylles ressemblent à ceux des feuilles, sauf que les premières n'atteignent pas 2% de la longueur du pétiole de la feuille adulte normale. On note une dégénérescence des tissus du limbe rudimentaire (Fig. 7A) pendant la période histogène et d'expansion. Il semble que dans certains cas (10%), l'une des cataphylles puisse continuer son développement comme une feuille normale. Cette deuxième feuille se trouve toujours à la même position dans l'organisation de l'appareil végétatif : elle suit directement la feuille de l'année courante (Fig. 8F).

Phase monopodiale. — Les spécimens juvéniles provenant des bulbilles ont un mode de croissance monopodial. Contrairement aux spécimens adultes, l'apparition de deux feuilles est commune chez les plants juvéniles cultivés en serre (45% des spécimens observés). D'après des travaux réalisées sur les *Anthurium* et les *Philodendron* (BLANC 1977a,b), la croissance monopodiale serait liée au stade juvénile tandis que la croissance sympodiale correspondrait au stade adulte étant donné que chaque article se termine par une inflorescence. Au stade de plantule, la première feuille du *D. polyphyllum* est pédalée et tripartite, comme cela a été rapporté chez les *Amorphophallus*. Par contre, chez les *Anchomanes*, la première feuille est entière et sagitée (KNECHT 1983). Cependant, selon KNECHT (1983), après la production d'une série de feuilles entières, le limbe se divise progressivement chez les *Anchomanes* pour finalement ressembler à celui des *Dracontium* et des *Amorphophallus*. Chez les spécimens juvéniles, il est difficile de préciser la position de la feuille de l'article suivant parmi les cataphylles, puisque l'ensemble des primordiums des cataphylles semblent avoir la possibilité de devenir une feuille.

Phase sympodiale. — Au cours d'un cycle annuel, la plante a une période de dormance entre sa feuillaison et sa floraison. C'est après la sénescence de la feuille que l'inflorescence apparaît, soit à la fin de la saison des pluies. Chez le *D. polyphyllum*, lorsqu'une inflorescence et une feuille se développent simultanément, cette dernière appartient à l'article suivant, c'est-à-dire celui qui se développera au prochain cycle phénologique (Tableau 2). Dans ce cas, l'inflorescence est à un stade de développement avancé, alors

que la sénescence de la feuille n'a pas encore débutée. Étant donné que, dans le cycle phénologique du *D. polyphyllum*, le développement de la feuille précède normalement celui de l'inflorescence, cette feuille plus jeune que l'inflorescence ferait donc partie de l'article suivant. Lors de la dissection du bourgeon terminal, il apparaît clairement que la structure qui émergera par la suite, donc celle ayant le stade de développement le plus avancé, sera une inflorescence et non une feuille. Ceci est différent de ce qui à été rapporté par KNECHT (1983) pour les *Anchomanes* et les *Amorphophallus* où la floraison précède la feuillaison. L'observation d'un spécimen conservé en serre appuie notre interprétation. Dans ce cas, le développement d'une nouvelle inflorescence suivra la présence simultanée d'une feuille et d'une inflorescence, et ce, sensiblement à la même date que pour des plants récoltés dans leur milieu naturel.

Lobation de la feuille. — Le limbe de la feuille mature du *D. polyphyllum* est divisé en trois parties égales ; celles-ci sont subdivisées en rachis secondaires, lesquels portent les folioles. Les trois rachis primaires portent aussi quelques folioles à leur base, sous le point d'insertion des rachis secondaires. Sur la jeune feuille encore protégée par une cataphylle, on observe un rachis central (antérieur), ainsi que deux rachis opposés l'un à l'autre (postérieurs), de moindre dimension que le rachis antérieur (Fig. 7B). Au cours du développement, les deux rachis postérieurs prennent de l'ampleur pour atteindre des proportions semblables au rachis antérieur. Ces rachis postérieurs ne sont pas des rachis secondaires, car chez les spécimens matures ils sont de forme et de proportion analogues au rachis antérieur.

Chez le *D. polyphyllum*, la lobation primaire se fait marginalement tandis que les dissections finales des feuilles montrent une lobation d'origine intramarginale (Fig. 7B-C). Le processus de lobation marginal implique l'alternance de régions de croissance (les folioles) et de régions sans croissance (les sinus). Par la suite, des sillons se creusent à une certaine distance de la marge foliaire pour finalement se romprent au cours de l'expansion et ainsi former les folioles (processus intramarginal). Un mode de développement analogue se rencontre aussi chez les Palmiers (KAPLAN et al. 1982). À cause de la présence de deux processus, le développement de la feuille du *D. polyphyllum* diffère de celui d'autres Araceae à feuille unique très découpée, telles que les *Amorphophallus* et les *Anchomanes*. En effet, d'après KAPLAN (1984), chez les *Amorphophallus* et la majorité des Araceae à feuilles fortement disséquées, il n'existerait qu'un processus d'initiation marginale. Dans le cas d'*Anchomanes*, HAY (1992) suggère que seul un processus d'initiation intramarginal interviendrait. Chez le *D. polyphyllum* on observe, dans certains cas, des folioles à fenestration. Cependant l'origine de ces fenestrations semble être une défaillance du processus intramatginal et non un phénomène de nécrose comme chez les feuilles à fenestrations typiques du *Monstera*, décrites par KAPLAN (1984) et MELVILLE & WRIGLEY (1969).

La feuille du *D. polyphyllum* se libère de sa cataphylle protectrice lorsqu'elle est encore à un stade de croissance peu avancé. Elle complétera donc son expansion exposée à l'air libre, hors de la cataphylle protectrice. Chez le *D. polyphyllum*, l'expansion foliaire est polaire, c'est-à-dire que le pétiole débute sa période de croissance sitôt après l'émergence de la feuille hors de la cataphylle. Ce processus se fait de façon acropète, tant en longueur qu'en diamètre. Durant cette période, le limbe de la feuille ne subit qu'une légère augmentation de taille. Les rachis gardent une orientation similaire à celle qu'ils avaient dans le bourgeon, c'est-à-dire que le rachis antérieur pointe vers le sommet et les rachis postérieurs pointent légèrement vers le bas. Progressivement, les rachis divergent à angle égal entre eux pour finalement prendre la forme d'un parasol. Cette période coïncide avec l'expansion et l'épaississement du limbe. Cette expansion foliaire tardive est rapportée pour plusieurs Araceae telles que les *Anchomanes*, *Gonatopus*, *Anthurium* et *Zamioculcas* (HAY & MABBERLEY 1991). Par contre, chez *Amorphophallus*, dont la feuille est à première vue semblable à celle du *D. polyphyllum*, on note que lors de l'émergence hors du sol, la feuille est beaucoup plus avancée dans son processus d'expansion. De plus, chez l'*Amorphophallus* le processus d'expansion est plutôt diffus, le pétiole et le limbe de la feuille se développant de façon synchrone (HAY 1992).

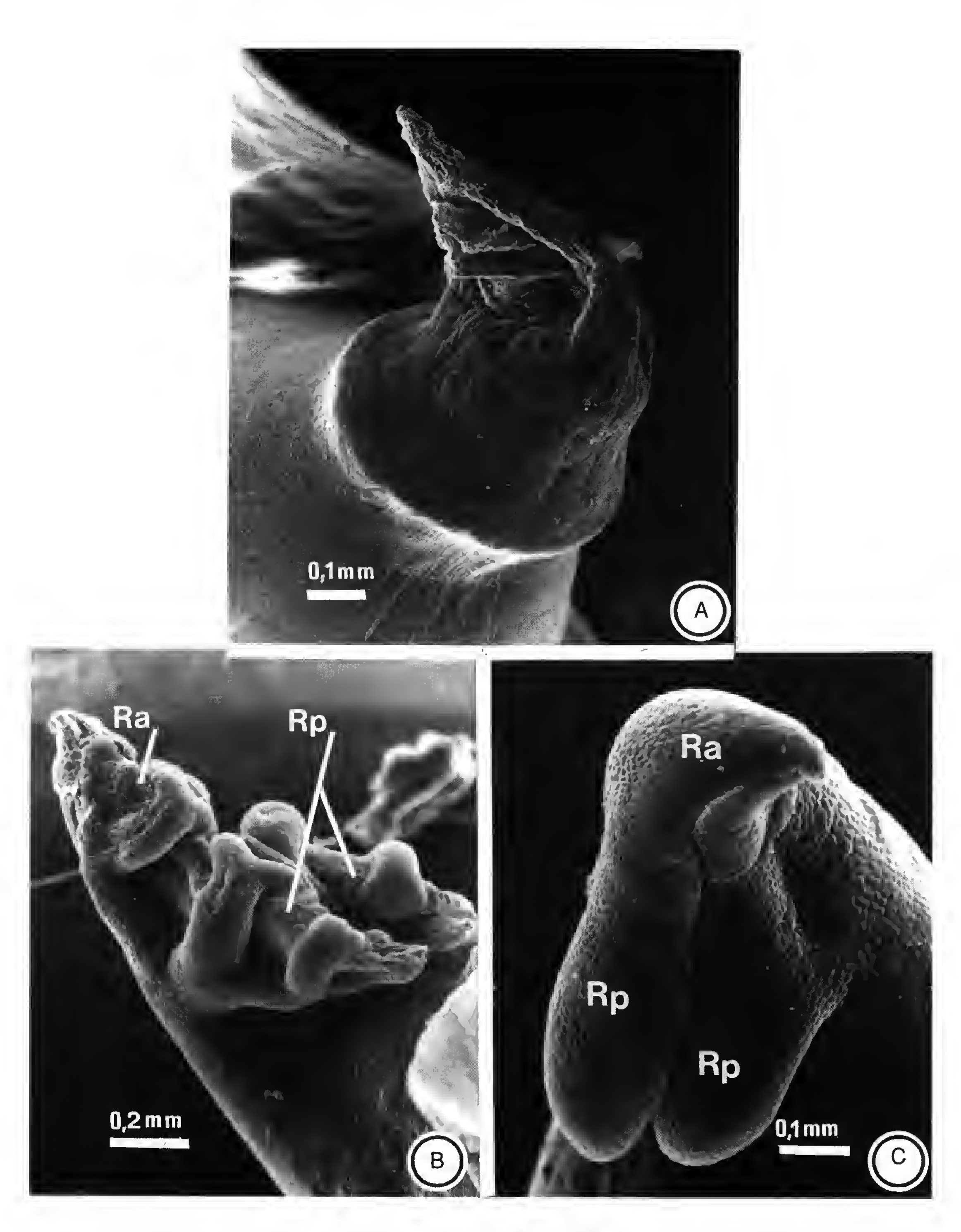


Fig. 7. — ***Dracontium polyphyllum*** : **A**, dégénérescence des tissus du limbe d'une cataphylle ; **B**, feuille en développement ; les dissections ultimes ont une origine intramarginale ; **C**, ébauche foliaire ; la lobation primaire est marginale. Ra, rachis central (antérieur) ; Rp, rachis opposé (postérieur).

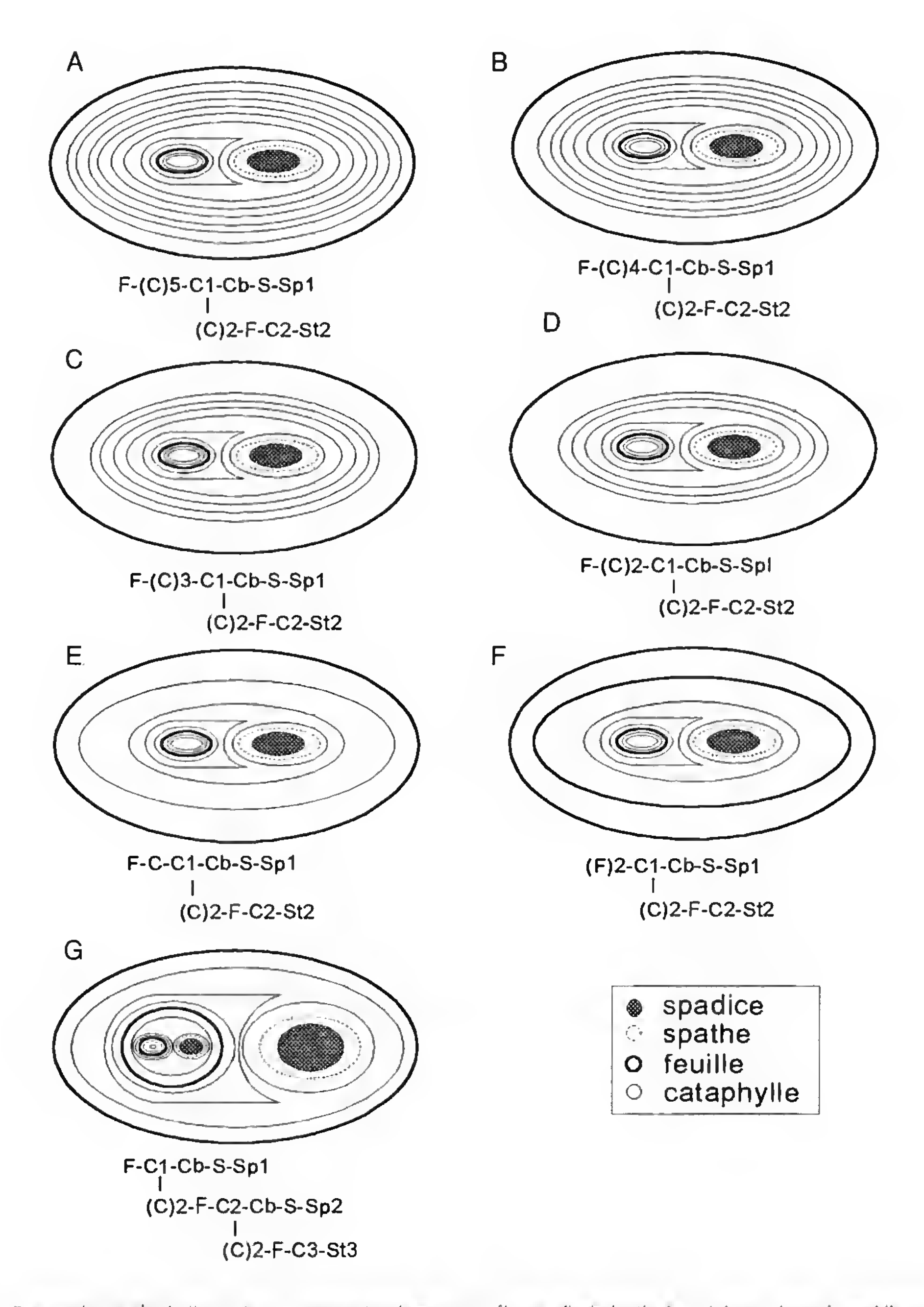


Fig. 8. — ***Dracontium polyphyllum***, diagrammes de l'architecture de l'appareil végétatif : **A**, spécimen observé quotidiennement de la floraison à la feuillaison (1995-96) ; **B**, spécimen disséqué sur le terrain (1994) ; **C**, **D**, spécimens disséqués sur le terrain (1994-95) ; **E**, spécimen disséqué sur le terrain (1995) ; **F**, spécimen à deux feuilles, disséqué sur le terrain (1994-95) ; **G**, spécimen portant une feuille et une inflorescence simultanément, disséqué sur le terrain (1994-95). Dans l'article de l'année suivante, il n'y a que deux cataphylles de représentées après la feuille, même si ce nombre peut être variable. — **Formule d'embranchement** : F, feuille ; C, cataphylle ; C1,2,3, cataphylle entourant l'inflorescence + prochain article, feuille, cataphylles et inflorescence de l'article 2 (le chiffre indique le cycle phénologique) ; Cb, cataphylle entourant l'inflorescence ; S, spathe ; Sp, spadice, St = (cataphylle + spathe + inflorescence), (le chiffre indique le cycle phénologique). Les parenthèses indiquent une répétition du même organe, le chiffre suivant la parenthèse indique le nombre de répétitions.

Diagrammes de l'architecture de l'appareil végétatif des spécimens adultes. — À partir des 47 diagrammes de l'appareil végétatif de spécimens adultes, nous avons déterminé 5 types d'organisation (Fig. 8). Le plus fréquent est celui où l'on dénombre 4 cataphylles sur le même article après la feuille de l'année courante, c'est-à-dire celle présente lors de la récolte (Fig. 8C). Ce mode de croissance se retrouve chez 54% des spécimens observés, nonobstant l'année et l'endroit de récolte. Les autres types d'organisation observés sont, par ordre d'importance : 5 cataphylles après la feuille chez 28% des spécimens observés (Fig. 8B), une (9%) (Fig. 8G), trois (5%) (Fig. 8D), deux (2%) (Fig. 8E) et 6 (2%) (Fig. 8A). Lorsque, sur un même article, il n'y a qu'une seule cataphylle après la feuille, on trouve, chez 50% des spécimens observés, deux feuilles dans l'année courante (Fig. 8F) et chez 66% une deuxième inflorescence à un stade de développement avancé (Fig. 8G).

ENGLER (1877) a classé l'organisation de l'appareil végétatif des Araceae en sept séries. Selon lui, le *D. polyphyllum* appartiendrait au type V de la septième série qui comprend de nombreux genres à tubercules comme les *Amorphophallus* et les *Anchomanes*. La classification de ENGLER repose largement sur la phyllotaxie et sur le type de croissance (grimpant, rampant, etc.). Dans le Tableau 1, se trouve détaillée la formule d'embranchement du *D. polyphyllum* donnée par ENGLER. Comme cette formule d'embranchement est une formule générale qui s'applique aussi à des espèces munies de plusieurs feuilles, la concordance exacte avec nos observations ne peut être absolue. Toutefois, il est possible de réunir les différentes formules d'embranchements que nous avons observées (Fig. 8) dans une formule générale (Tableau 2). Si l'on transpose la formule du Tableau 2 dans la notation de ENGLER on obtient une formule qui pourrait à la rigueur être incluse dans la formule générale de ENGLER (Tableau 3).

Le nombre de cataphylles après la feuille de l'article suivant ne peut être déterminé précisément lors de la dissection. Le nombre de cataphylles qui se développeront sur l'article du cycle suivant variera en fonction de facteurs liés à l'environnement. Par exemple, les spécimens cultivés en serre ont tous développé un grand nombre de cataphylles entre la feuille et l'inflorescence, tandis que ceux disséqués sur le terrain avaient généralement moins de cataphylles. Ce phénomène pourrait s'expliquer par le fait que, lors du transport du tubercule, nous avons prématurément enlevé la feuille de l'année courante. Nous croyons que cette résection aurait provoqué une augmentation du nombre de cataphylles dans les articles suivants.

Comme l'a noté JEANNODA-ROBINSON (1977), certains modèles architecturaux définis chez les arbres par HALLÉ & OLDEMAN (1970) se retrouvent d'une façon miniaturisée chez les herbacées. Ces auteurs utilisent trois critères architecturaux pour définir leurs modèles : 1) l'orientation de croissance des axes végétatifs, 2) les caractéristiques de la croissance des axes, 3) la position des fleurs ou des inflorescences. Dans le cas du *D. polyphyllum*, nous sommes en présence d'une miniaturisation du modèle de Chamberlain, comme chez les Araceae en général (RAY 1987b ; HAY 1992). Dans ce modèle, une succession indéfinie d'articles, dérivant les uns des autres par un mécanisme sympodial, se renouvelle à chaque cycle de croissance. Chaque article apparaît de façon acrone à partir d'un bourgeon situé sous l'inflorescence terminale. Ce modèle ne s'appliquerait qu'imparfaitement aux *Amorphophallus* qui correspondent au modèle mixte de

TABLEAU 1. — Formule d'embranchement de l'organisation de l'appareil végétatif, 7ème série, type v de la classe des espèces à tubercules souterrains, selon ENGLER (1877). N, cataphylle ; L, feuille ; N(n-1), cataphylle qui entoure l'inflorescence et l'article suivant (*next higher shoot order*) ; Nn, cataphylle qui entoure l'inflorescence ; S, spathe ; Sp, spadice. Les parenthèses indiquent une répétition possible de l'organe.

```
7e série, Type V :
          N,N,N,.(L,L).L,N,N.......N(n-1),Nn,S,Sp.
                                    |
                                    N,N,N...(L,L),L,N,N,....N(n-1),Nn,S,Sp.
```

TABLEAU 2. — Formule d'embranchement de l'organisation de l'appareil végétatif du *Dracontium polyphyllum*. F = feuille ; C = cataphylle ; C1, C2 = cataphylles qui entourent l'inflorescence et l'article suivant (*next higher shoot order*) ; Cb = cataphylle qui entoure l'inflorescence ; S, spathe ; Sp, spadice. Les parenthèses indiquent une répétition du même organe, l'indice donne le nombre de répétitions possible.

$$
\begin{array}{l}
(F)1\text{-}2 - (C)_{0\text{-}5} - C1 - Cb - S - Sp \\
\qquad\qquad\qquad\quad | \\
\qquad\qquad\qquad\quad (C)_{0\text{-}5} - F - C2 - Cb - S - Sp
\end{array}
$$

TABLEAU 3. — Formule d'embranchement du Tableau 2 transposée dans la notation de Engler (1877).

N,N,(L),L, N,N...N(n-1),Nn, S,Sp.
|
N,N,L,N,N...N(n-1), Nn, S,Sp.

Chamberlain/Tomlinson (BLANC 1978, 1986). Comme dans le modèle de Chamberlain, les *Amorphophallus* se caractérisent par une succession indéfinie d'articles qui se renouvellent à chaque cycle de croissance et dérivent les uns des autres par un mécanisme de croissance sympodial ; cependant, plutôt que de provenir du sommet de l'article précédent, le nouvel article émerge de sa base. Cette caractéristique propre au modèle de Tomlinson explique l'appellation du modèle. La différence entre ces deux genres, au niveau de l'architecture de l'appareil végétatif, pourrait être liée à des variations dans leur cycle de croissance. Seule une étude détaillée de l'architecture de l'appareil végétatif des *Amorphophallus* permettra de vérifier cette hypothèse. Soulignons cependant qu'il est très délicat d'émettre des généralités pour le genre *Amorphophallus* quand on sait qu'il renferme une centaine d'espèces, dont très peu ont été étudiées sous ces aspects. Rappelons, à ce sujet, que PATE & DIXON (1982) décrivent une espèce monocarpique, l'*Amorphophallus glabra*, qui est donc conforme au modèle de Holtrum, selon la classification de HALLÉ & OLDEMAN (1970).

RAY (1987a,b ; 1988) a proposé une classification des différents types d'organisation de l'appareil végétatif des Araceae. Si l'on adopte cette classification, le *D. polyphyllum* aurait une organisation de type anisophylle proleptique ; anisophylle, puisqu'on trouve chez cette espèce un nombre variable de feuilles (incluant les cataphylles) et proleptique, car un nouvel article ne se développe qu'après une période de repos du bourgeon apical. D'après RAY (1987b), ce type d'organisation n'a été, jusqu'à maintenant, observé que chez les *Philodendron* sect. *Pteromischum* ; toutefois, selon RAY (1988), cette organisation existerait aussi chez plusieurs espèces de *Monstera*. Le *D. polyphyllum* peut, dans certains cas, développer une deuxième feuille simultanément avec l'inflorescence (Fig. 20G). Dans ces cas exceptionnels, il semble qu'il adopte momentanément une organisation de l'appareil végétatif de type anisophylle sylleptique, puisque le nouvel article provient d'un bourgeon apical qui n'a pas été soumis à l'effet d'une période de repos.

Selon TOMLINSON (1982), les espèces d'Aracées géophytiques seraient néoténiques. La croissance du *D. polyphyllum* est caractérisée par une période juvénile où la feuille est peu disséquée et une période adulte plus longue et permanente, caractérisée par une croissance sympodiale et une feuille très découpée (Fig. 4). On observe un type de croissance semblable chez les espèces d'*Amorphophallus* et d'*Anchomanes*. Or, ces espèces géophytiques ne présentent pas de retard dans le développement somatique, ni d'accélération de la maturation. On ne peut donc parler de néoténie, comme le suggère TOMLINSON (1982). Il faudrait plutôt parler de croissance télescopique où les unités architecturales sont enchaînées et répétitives (BARABÉ 1987).

CONCLUSION

Même si la morphologie des *Dracontium* ressemble à celle des *Amorphophallus* et des *Anchomanes*, ces trois genres présentent certaines différences tant sur le plan de l'organisation végé-

tative que florale. Chez le *D. polyphyllum*, le mode de lobation de la feuille est marginal et intramarginal, tandis que, d'après les données bibliographiques, il serait uniquement marginal chez *Amorphophallus* et uniquement intramarginal chez *Anchomanes*. On remarque également que le processus d'expansion foliaire est polaire chez le *D. polyphyllum* alors qu'il serait diffus chez l'*Amorphophallus*. Chez le *D. polyphyllum*, l'expansion de la feuille se déroule à un stade de développement plus précoce que chez l'*Amorphophallus*. Enfin, la feuillaison a lieu avant la floraison chez le *D. polyphyllum*, tandis que ce serait le contraire chez les *Amorphophallus* et les *Anchomanes*.

Du point de vue architectural, le *D. polyphyllum* peut être classé dans trois catégories différentes selon le cadre théorique adopté. Selon la classification d'ENGLER (1877), cette espèce correspond au type V de la septième série. D'autre part, si l'on adopte la classification architecturale d'HALLE & OLDEMAN (1970), le *D. polyphyllum* correspond au modèle de Chamberlain, comme la plupart des Araceae. Finalement, d'après la classification de RAY (1987), le *D. polyphyllum* a une organisation de type anisophylle proleptique, ce qui a été peu observé chez les Araceae.

Malheureusement, aucune étude comparative détaillée de l'organogenèse de la feuille des Araceae géophytiques n'a encore été réalisée. En conséquence, il serait intéressant d'effectuer pour les genres *Dracontium*, *Amorphophallus* et *Anchomanes* une analyse approfondie de la morphogenèse foliaire en relation avec le mode de croissance et l'architecture de l'appareil végétatif.

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Encephalartos ituriensis (Zamiaceae): an emended description

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ABSTRACT
The original description of *Encephalartos ituriensis* (Zamiaceae) is incomplete, to some extent inaccurate and based in part on immature material. Based on subsequently collected material and on observations in situ, an emended description with illustrations of the fronds and mature female cones is provided.

KEY WORDS
Encephalartos ituriensis, Zamiaceae, D.R. Congo

RÉSUMÉ
La description originale d'*Encephalartos ituriensis* (Zamiaceae) est incomplète, parfois inexacte, et en partie fondée sur un matériel immature. Grâce à des échantillons récoltés postérieurement et aux observations de terrain, une description amendée, avec des dessins de frondes et de cônes femelles mûrs, est présentée.

MOTS CLÉS
Encephalartos ituriensis, Zamiaceae, R.D. Congo

The original description of *Encephalartos ituriensis* Bamps & Lisowski (BAMPS & LISOWSKI 1990) was fairly detailed, but many of the data presented there were ambiguous or incomplete, to the extent that when the second author saw plants in nature, he thought that they could represent a different species. The size of the female cone given in the protologue is incorrect and the information given concerning the surface sculpturing of the exposed faces of the sporophylls is ambiguous. No information was given concerning the color of male and female cones, the presence or absence of a petiole, the indumentum of the cones, the texture of the leaflets, and the distribution of teeth on the leaflets, all characters considered diagnostic by VORSTER (1990 and in press). No illustrations of any part of the mature frond were given; only a line draw-

ing was provided of a seedling plant with two leaves. GOODE (1989: 229-231) published detailed color plates of a whole plant, leaflets, cones, and sporophylls, purportedly of *E. ituriensis*, in the year before the valid publication of the binomial. However, the provenance of the material illustrated cannot be established. GOODE's habit illustration was based on a photograph of a cultivated plant growing on the shore of Lake Kivu and said to be from the Ituri Forest. The cones that he illustrated are from a different plant and were received from a collector in Zimbabwe without any locality data. GOODE (1989: 230) provided no scale of magnification for the illustrations of the leaflets, and the dimensions of 20 × 12 cm given for the female cone (GOODE 1989: 231) are obviously incorrect considering the relative size of the stem apex and frond bases attached.

The type material as well the additional specimens cited by BAMPS & LISOWSKI (1990) all come from near Nduye in the northeastern Democratic Republic of Congo. After consideration of the original description, allowance for missing and possibly inaccurate information, and study of *Lisowski 41057* (BR) and herbarium specimens and photographs of *Gereau et al. 5413* (Democratic Republic of Congo, near Nzaro, ca. 30 km northwest of Nduye; EA, epu [reference collection at Epulu], MO, PRE), we conclude that all of these specimens are conspecific. Therefore, it is clear that the markedly small female cones reported for *E. ituriensis* by BAMPS & LISOWSKI (1990) were either depauperate or not fully developed and that the circumscription of the species in the protologue is inadequate. Accordingly we supply the following emended description:

Encephalartos ituriensis Bamps & Lisowski **emend.** Vorster & Gereau

Plant arborescent, palm-like in shape, unbranched but sometimes suckering from base; stem to 6 m long and 40-50 cm thick, usually procumbent with apical portion erect when more than 2 m long, covered with leaf base remains in a regular pattern, the apex glabrous except for floccose tawny indumentum on cataphylls. Fronds numerous, spreading-ascending in a hemispheric crown, straight, dark glossy green, 2-3 m long, sessile; base of rachis covered with short tawny floccose indumentum; leaflets ca. 80 pairs, gradually reduced to a series of prickles toward base of frond; median leaflets in plane view oriented at angle of ca. 60° with rachis and pointing toward frond apex, opposing leaflets set at angle of slightly less than 180° to each other on circumference of rachis, narrowly oblong-lanceolate and tapering to acute but not pungent apices, not or slightly falcate, with (3-)4-6(-9) teeth rather evenly distributed along both margins and ca. 3 teeth crowded near base of distal margin, in dried specimens finely corrugated on abaxial surface and margins (including margins of teeth), revolute, not or only slightly overlapping, somewhat soft-textured, 19-30 × 2-3 cm (excluding teeth). Male cone [not seen, description from BAMPS & LISOWSKI (1990)] number unknown, narrowly ellipsoid, borne on a stout peduncle to 16 cm long and 1.8 cm thick, color not recorded but presumed similar to female cone (see below), glabrous, [in dried state?] ca. 26 × 7 cm; exposed faces of male sporophylls moderately projecting, slightly drooping at maturity, ca. 2.5 mm wide, the terminal facet differentiated, rhombic, its diameter ca. 60% of total horizontal diameter of exposed face; female cones 1-4, ovoid-cylindrical at maturity, borne on a peduncle ca. 10 cm long, initially glaucous-green becoming yellow-green at maturity, glabrous, ca. 55 × 20 cm; exposed faces of female sporophylls raised, somewhat pyramidal, ca. 7 × 4.5 cm, the terminal facet off-center toward base of cone, its diameter 25-33% of total horizontal diameter of exposed face, the median facet differentiated, with ridges separating facets clearly differentiated; facets smooth on faces when fresh, tuberculate when dry, margin of exposed face of fresh sporophyll tuberculate. Seed with sarcotesta red when fresh, brown when dry, 37-39 × 21-28 mm with dried sarcotesta intact, 36-38 × 20-25 mm with sarcotesta removed.—Fig. 1, 2.

GEOGRAPHICAL DISTRIBUTION AND HABITAT

Encephalartos ituriensis is known with certainty only from the Ituri Forest in the Democratic

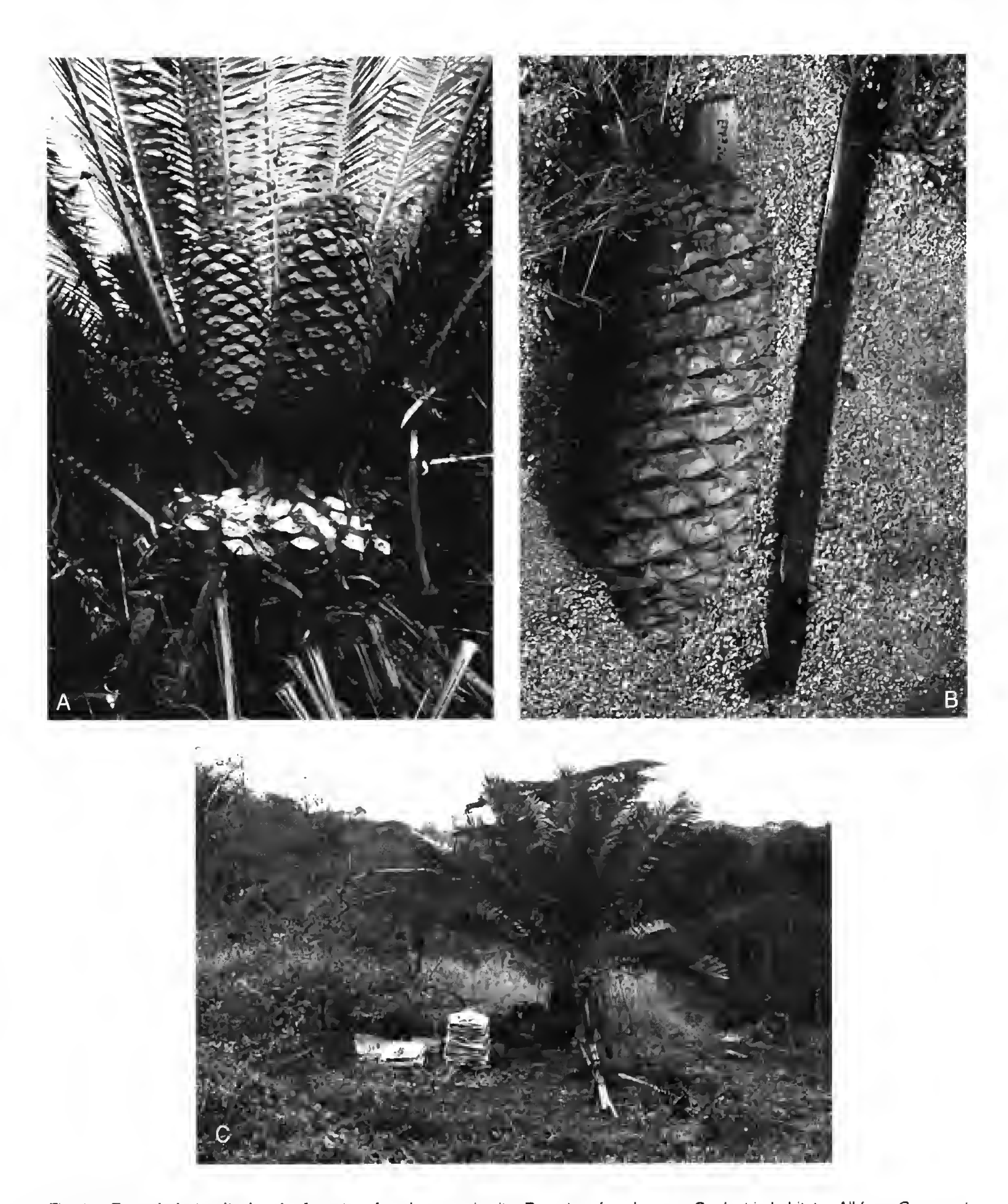


Fig. 1.—***Encephalartos ituriensis***: **A**, mature female cones in situ; **B**, mature female cone; **C**, plant in habitat.—All from *Gereau et al. 5413*.

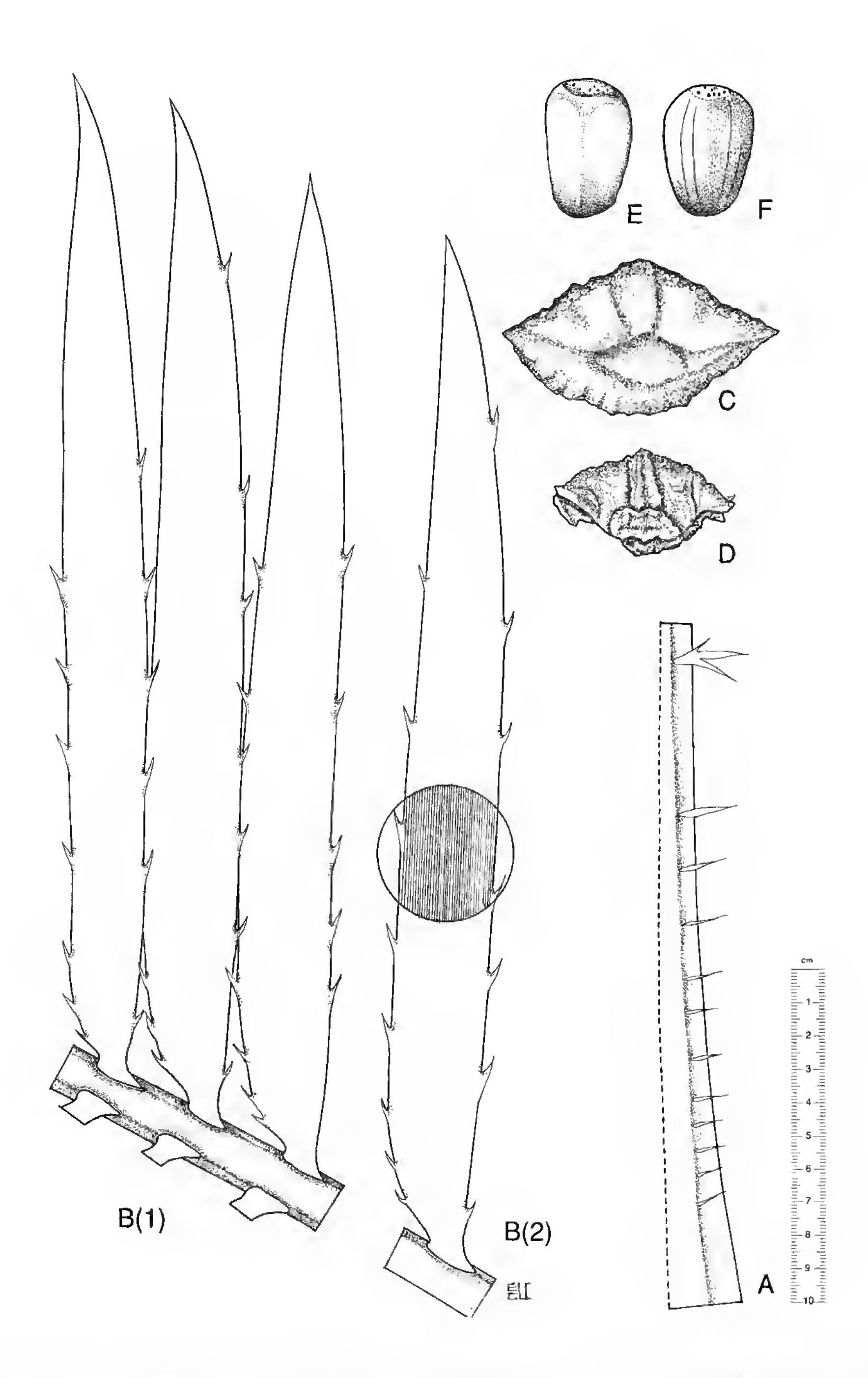


Fig. 2.—***Encephalartos ituriensis***: **A**, basal part of rachis showing leaflets reduced to a series of prickles; **B**, median leaflets in (1) adaxial and (2) abaxial view; **C**, exposed face of fresh female sporophyll, showing well-defined and smooth facets; **D**, exposed face of dried female sporophyll, presenting a tuberculate aspect; **E**, seed with sarcotesta intact; **F**, seed with sarcotesta removed (scale bar = 10 cm).—All from *Gereau et al. 5413*.

Republic of Congo at altitudes of 1100-1200 m, from five localities forming an arc over a distance of some 160 km from near Nzaro south-eastwards to near Nyankunde, with coordinates 1-2°N-28-30°E. For considerations of conservation we do not publicize the localities in greater detail. While most of the surrounding area supports a mosaic of mixed moist and single-dominant moist semi-evergreen Guineo-Congolian rain forest (WHITE 1983), the habitat of *Encephalartos ituriensis* lies outside the forest at somewhat higher elevations on exposed granitic domes that support a xerophytic flora with a number of disjunct and possibly endemic elements (LISOWSKI 1992). At one locality *E. ituriensis* grows among grass in savanna-like vegetation, but this is apparently a degraded secondary formation that has been altered by grazing of domestic livestock.

PHENOLOGY

Male cones are known only from April (*Lisowski 42234*), and female cones only from March (*Gereau et al. 5413*) and April (*Lisowski 42909*). The strong seasonality of the annual rainfall regime in the Ituri Forest (HART et al. 1996: 547), and additionally the edaphic dryness of the extremely well-drained sites within this formation on which *Encephalartos ituriensis* occurs, make it probable that growth and seed production are regulated by precipitation patterns. The months of March and April correspond to the end of the single dry season and the beginning of the rains.

DIAGNOSTIC FEATURES AND AFFINITIES

Geographically *Encephalartos ituriensis* occurs closest to *E. whitelockii* P.J.H. Hurter of western Uganda, but these species are separated by the Rift Valley, which probably represents a strong isolating factor. They share glaucous-green cones that at least sometimes turn yellow at maturity (HURTER 1995), long-peduncled male cones, more or less smooth and glabrous exposed faces of female sporophylls, and leaflets that overlap little or not at all (VORSTER & HEIBLOEM 1995, as *E. successibus* Vorster). *Encephalartos whitelockii* differs from *E. ituriensis* in its hard- instead of soft-textured leaflets without a concentration of teeth near the base of the distal margin of each leaflet, and more numerous male cones, up to 8 borne together.

The only other near-equatorial African species with soft-textured leaflets is *Encephalartos laurentianus* De Wild., from the Kwango River valley bordering the Democratic Republic of Congo and Angola. This is a larger species, which can be distinguished by its larger leaflets (up to 50 × 5 cm), long-peduncled female cones, and a reddish indumentum on the cones of both sexes (DE WILDEMAN 1903: 10; 1904: 392; BOIS 1907; GENTIL 1904a,b; LEBRUN 1930).

DISCUSSION

Our emended circumscription of *Encephalartos ituriensis* excludes the illustrations by GOODE (1989: 229-231) for the reasons given above. We extend the diagnostic characters used to recognize the species, and include a larger range of morphological variation than originally described by BAMPS & LISOWSKI (1990). Much of the additional morphological variation is due to the plants from Nzaro (cf. *Gereau et al. 5413*), which are larger and more luxuriant than those at Nduye (cf. *Lisowski 41057*). The Nzaro plants have longer median leaflets with more acute apices and much larger female cones, but the morphological differences between the populations appear insufficient to justify separate taxonomic status.

Acknowledgements

The second author thanks John and Terese HART for their enthusiastic support and warm hospitality during his visits to the Ituri Forest, and Charlotte TAYLOR and Gordon MCPHERSON for critical reading of the manuscript. The first author's research was funded by the Research Fund of the University of Stellenbosch.

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Analyse d'ouvrages — *Book reviews*

L.J. Dorr. *Plant Collectors in Madagascar and the Comoro Islands. A biographical and bibliographical guide to individuals and groups who have collected herbarium material of algae, bryophytes, fungi, lichens and vascular plants in Madagascar and the Comoro Islands.* Préface de Césaire RABENORO. Introduction de Ghillean PRANCE. The Trustees, Royal Botanic Gardens, Kew, 1 vol., xlvi + 524 p., ISBN 1 900347 18 0 (1997).

En s'engageant dans cette recherche, sans doute Laurence J. DORR, alors au Missouri Botanical Garden et actuellement au département de botanique de la Smithsonian Institution, n'imaginait pas l'ampleur de la tâche à accomplir. Il en résulte un ouvrage exceptionnel dans la bibliographie botanique, même si quelques excellentes contributions antérieures ont tracé la voie, telles celles de GAGNEPAIN pour l'ancienne Indochine (avec portraits, 1943), de LETOUZEY pour le Cameroun (1968), de HEPPER pour l'Ouest Africain (1971), ou celle de VAN STEENIS pour Flora Malesiana (1950), entre autres.

La présente synthèse prend une plus grande ampleur du fait qu'il s'agit en fait d'une « bio-bibliographie » commentée des récolteurs ayant opéré sur le territoire considéré, depuis les origines (E. DE FLACOURT 1648) jusqu'au milieu des années 1990. Après quelques pages de données techniques, on trouve une très importante bibliographie générale pp. xvii-xxxiii, un commentaire (+ carte) sur les espaces protégés de Madagascar, une liste des herbiers et collections xylologiques non citées dans l'ed. 8, 1990, de l'Index Herbariorum, puis un Index d'abréviations et symboles utilisés. L'Index des récolteurs est présenté alphabétiquement, chaque lettre s'ouvrant sur la photographie d'un paysage, botanique ou autre, typique de la région. Pour chaque récolteur, on trouve (si cela est connu, ou si c'est la cas) : nom et prénom(s), dates et lieux de naissance et décès, « cursus », activités botaniques (ou générales), à Madagascar ou dans d'autres régions, éponymie(s) génétiques, références bibliographiques. Concernant la personne, références de portraits (au trait, peints, photos), dates des récoltes à Madagascat et aux Comores, sources de manuscrits, herbiers où sont déposées des collections. Bien entendu, les nationalités sont mentionnées et l'un des grands intérêts de ces biographies est d'avoir recherché le mieux possible les contributions des Malgaches à la connaissance de la flore de leur pays au travers des récoltes qu'ils ont pu faire eux-mêmes, ou aider à réaliser. Si les voyageurs-naturalistes ont une place affirmée, on relèvera que nombre de forestiers, agronomes, administrateurs, etc. contribuèrent à réunir les collections botaniques dont nous disposons aujourd'hui et qui sont l'indispensable outil de travail pour les connaissances systématiques et l'évaluation de la diversité floristique (et parfois de ses pertes, parallèlement aux découvertes faites chaque année). Une marge blanche en bordure de page a permis l'insertion de nombreux portraits des récolteurs mentionnés ; mais il est bien évident que dans ce domaine, beaucoup de visages demeurent inconnus ; on a même démontré récemment que le portrait de Ph. COMMERSON (p. 93) ne représentait pas le naturaliste de l'expédition de Bougainville ! Les choix sont donc parfois fort difficiles et c'est ce qui explique en partie certaines lacunes lorsque les recoupements ne permettaient pas de parvenir à une certitude raisonnable. Excellemment présenté, bien lisible malgré la densité des textes, l'ouvrage de Laurence J. DORR procure un véritable plaisir aux lecteurs intéressés à l'histoire de la botanique, pas seulement pour Madagascar et les Comores (!). C'est aussi un hommage rendu à des investigateurs parfois oubliés ou méconnus qui ont joué un rôle dans la trame complexe des explorations. Un exemple en est donné dans les dernières pages, avec la liste de plus de 500 collaborateurs des Services forestiers. La livraison inclut un CD.

On ne peut qu'être reconnaissant à l'auteur et aux autorités de Kew pour l'édition de cet ouvrage extrêmement documenté qui, même si des améliorations peuvent enrichir des éditions ultérieures, pourra faire regretter à beaucoup que rien de semblable n'existe pour la France !

G.G. AYMONIN

F.G. Brieger, R. Maatsch & K. Senghas (eds.). "*Rudolf Schlechter. Die orchideen*", 3rd ed. Band I/B, 31. Lieferung. Blackwell Wissenschafts-Verlag, Berlin & Parey Verlag, Hamburg, 1905-1976 pp., figs. 1866-1947. Paper cover, format 18.8 × 28.5 cm (1995).

Rudolf SCHLECHTER (1875-1925) was a great German botanist and traveller connected with the famous museum and botanic garden in Berlin-Dahlem. At first he was employed as a gardner, and later as a curator of the herbarium. Orchids were a real passion of his life, and he collected them during numerous trips to the tropics. One of his greatest works is the famous "Die Orchideen" published in Berlin in 1914, which contains a synthesis of all the knowledge of thar time on orchids. Soon after SCHLECHTER's death in 1927, the second, revised and updated edition of this work was published. In 1970 BRIEGER, SENGHAS & MAATSCH initiated the third edition of "Die Orchideen", which is completely different from the first edition and includes two volumes. The first is a taxonomic description and consists of three parts; the second, published in 1985, describes orchids as horticultural plants and problems connected with their cultivation.

"Die Orchideen" is to this day the only taxonomic treatment containing keys for determination of all genera, and in many cases also species, especially the ones of particular importance in cultivation mentioned in this work. "Die Orchideen" includes numerous, good quality black and white photographs showing representatives of most genera. However, the many ink illustrations are not of equal quality, especially those published in the first chapters.

Fascicle 31, discussed here, is in fact the final portion of part B of the first volume. It includes the following taxa: 5 genera of subtribe Ornithocephalinae and also 6 subtribes (Pachyphyllinae, Pterostemmatinae, Raycadencoinae, Lockhartiinae, Trichocentrinae and Ionopsidinae) of tribe Oncidieae, gathered in an informal group "Tribella Bipolliniata", all belonging to subfamily Vandoideae.

Orchids of subfamily Vandoideae, which are more or less related to *Oncidium*, are the most numerous group in the neotropics. They are said to include about 1500 species belonging to almost 100 genera. Their classification has evoked lively discussion among taxonomists for years. The most recent attempt to classify members of the *Oncidium*-alliance done by DRESSLER (1993) seems to be unacceptable, because the author treats all these genera within the large subtribe Oncidiinae. SENGHAS used a more practical rather than phylogenetic approach to this problem, dividing Oncidieae into two series of subtribes based on the number of pollinia, without paying attention to such important features in systematics of Vandoideae as for example rostellum, tegula and viscidium structure. Therefore, according to SENGHAS, Oncidieae include among others Stanhopeinae, orchids that, due not only to their gynostemium structure but also the architecture of their vegetative parts, seem to be more closely related to Oncidieae than, for example, to Maxillarieae.

However, SENGHAS's classification is also different from the one suggested by me (SZLACHETKO 1995), among others, due to the way in which he classifies subtribes Ornithocephalinae and Pachyphyllinae.

The other taxa in the "Tribella bipolliniata" group were divided by SENGHAS into 13 subtribes, of which Raycadencoinae was described as new. The taxonomic concept of those subtribes is in many cases the same as mine, and the differences concern the systematic position of several genera. It is worth mentioning that SENGHAS considered *Orchidotypus* Kraenzl. as a separate genus, although it is usually treated as a synonym of *Pachyphyllum* Kunth.

Parr C of rhe firsr volume, which is to be published in near future, will include the other taxa of

Vandoideae, supplements, an index and a listing of the literature that was used in the work. Altogether the third edition of "Die Orchideen" will contain about 3200 pages with thousands of photographs and hundreds illustrations. It will be the most comprehensive treatment that has ever been published on orchidology. Unfortunately, like every work published over a long period of time, it may nor contain all of the most recent taxonomic news; of which there is a lot in this group. I hope that the editors will express their views on at least some of them in the last part of their work.

D.L. SZLACHETKO

T. Shimizu (ed.). *Flora of Nagano Prefecture.* Shinano-mainichi Press, Nagano, Japan, 1 vol., 1735 p., illustr., ISBN 4-7840-9725-2, format A4 (1997).

Ce volumineux ouvrage, en japonais essentiellement, est une œuvre collective réalisée en une vingtaine d'années sous la direction du Prof. SHIMIZU avec la collaboration de plusieurs botanistes japonais de la Société botanique de la Préfecture de Nagano.

Une première partie introductive comprend : une collection de belles photographies en couleur (p. III-X) représentant des plantes vasculaires des différentes zones de végétation (alpine, subalpine, montagnarde, collinéenne et aquatique) ; une préface de T. SHIMIZU (p. XI-XII) ; des remarques sur la façon de lire l'ouvrage (p. XIII-XV) avec une carte des 12 sous-préfectures ; le sommaire détaillé jusqu'au niveau de la famille en japonais et latin (p. XVI-XX).

La fraction principale est subdivisée en 4 parties : partie 1 (p. 1-50) : conditions écologiques (géographie, géologie, climat, types de végétation) ; partie 2 (p. 51-124) : historique de la Flore (botanistes et périodiques ayant étudié la flore de la Préfecture de Nagano) ; partie 3 (p. 125-1544) : Flore proprement dite (sélection d'Algues principalement planctoniques ; Bryophytes limitées au genre *Sphagnum* dont toutes les espèces sont décrites, figurées et identifiables à l'aide de clés dichotomiques ; Ptéridophytes avec clés de détermination des familles, genres, espèces, dessins d'illustration et cartes de distribution ; Gymnospermes et Angiospermes étudiées exhaustivement comme les Ptéridophytes ci-dessus. Les 51 nouveautés scientifiques de la flore sont énumérées en latin. L'utilisation d'un ordinateur et de fiches perforées pour la détermination des familles et des espèces de cette Flore est expliquée. Enfin, partie 4 (p. 1545-1674) : Phytogéographie ; considérations concernant le passé et le présent ; guides botaniques pour les 12 sous-régions de la préfecture ; monuments naturels). Des index en japonais et en latin terminent l'ouvrage.

Sont jointes à ce document trois cartes en grand format, une topographique, une géologique en couleurs et une des types de végétation également en couleurs.

L'analyse résumée qui vient d'être exposée révèle une somme de connaissances peu ordinaire pour une Flore locale. Nul doute que les amateurs et les scientifiques japonais puissent en tirer le meilleur profit et y trouver des informations qu'une Flore plus générale ne pourrait pas leur donner, en particulier en ce qui concerne la distribution géographique des espèces ici minutieusement reportée à l'aide d'un quadrillage particulier. Les botanistes occidentaux, s'ils ne peuvent pas, en raison de la langue, comprendre et utiliser toutes les informations de cette Flore, pourront cependant admirer les 46 photographies en couleur de quelques paysages végétaux et plantes de la préfecture de Nagano sans toutefois en comprendre les légendes en japonais et, grâce aux noms latins, se faire une idée suffisamment précise de la composition floristique de cette région. Ils sauront particulièrement gré au directeur de cette Flore d'avoir rappelé dans la partie historique le rôle pionnier de botanistes occidentaux qui ont commencé à défricher le terrain vierge de la connaissance botanique du Japon et d'avoir inséré leur portrait dans les pages de cette Flore.

En résumé, on retiendra que cette Flore de la Préfecture de Nagano est un bel ouvrage, très bien documenté et digne de figurer dans toute bibliothèque spécialisée.

J.E. VIDAL

J. Florence. *Flore de la Polynésie française.* Ed. ORSTOM, vol. 1, 393 p., 50 fig., 4 p. photos, 2 cartes (1997).

C'est en 1982 que le territoire de la Polynésie française demanda à l'ORSTOM, aujourd'hui l'Institut Français de Recherche Scientifique pour le Développement en Coopération, de réaliser une flore moderne de ces îles. Cette étude fut confiée à Jacques FLORENCE qui venait d'être recruté par l'Institut.

La flore de la Polynésie française de DRAKE DEL CASTILLO, datant de 1893 et la Flore of South-Eastern Polynesia de F.B.H. & E.D.H. BROWN réalisée après 1922, ne répondaient plus aux besoins de connaissances plus précises sur la flore et la végétation des îles. Un travail important sur le terrain devait d'abord être réalisé pour réunir les observations et le matériel d'étude nécessaires. J. FLORENCE s'y est consacré pendant une dizaine d'années avec beaucoup de persévérance et de courage, la prospection des parties montagneuses des îles n'étant pas de tout repos. Un herbier de plus de 10.000 échantillons a été constitué qui, avec les collections plus anciennes existant dans divers grands herbiers mondiaux, a formé la base de l'étude floristique.

La flore totale des Phanérogames de la dition est estimée à 675 espèces, ce qui parait peu comparé à d'autres îles, il est vrai plus étendues, comme la Nouvelle-Calédonie ou les Hawaï. Son intérêt réside dans le fait qu'environ les 3/4 des espèces sont endémiques.

Nous saluons ici avec beaucoup d'intérêt et de sympathie, la sortie du 1er volume de cette flore, réalisé entièrement par J. FLORENCE. L'ouvrage compte 393 pages. Dans l'introduction, l'auteur brosse le cadre phytogéographique, donnant des renseignements sur la flore et la végétation des différents archipels constituant la Polynésie française. L'histoire de l'exploration botanique des îles est aussi détaillée, et une bibliographie concernant surtout la végétation est donnée, ainsi que la liste des abréviations qui sont utilisées pour l'ensemble de la flore. L'auteur a choisi de placer à la fin de l'ouvrage une clé des familles des Dicotylédones, ainsi que le glossaire des termes botaniques, et la liste des échantillons étudiés avec leur localisation.

Sept familles sont traitées : Cannabaceae, Cecropiaceae, Euphorbiaceae, Moraceae, Piperaceae, Ulmaceae, Urticaceae. Au total 113 espèces endémiques, indigènes et naturalisées et 55 espèces cultivées. Les Cannabaceae et Cecropiaceae ne comprennent chacune qu'une espèce introduite. Les Euphorbiaceae constituent une des familles les plus importantes pour les îles polynésiennes, avec 13 genres, 59 espèces endémiques, indigènes et naturalisées et 25 espèces cultivées. Le genre *Glochidion* présente une spéciation très poussée avec 22 espèces endémiques. Les Moraceae, avec 7 genres et 8 espèces indigènes ou naturalisées mais aucune endémique, ont un moindre intérêt. Les Piperaceae comptent 3 genres et 17 espèces indigènes ou endémiques, 3 espèces naturalisées et quelques espèces cultivées ; 10 espèces, toutes des *Peperomia*, sont endémiques. Les Ulmaceae forment une petite famille de 3 genres représentés chacun par une espèce ; une espèce est indigène et deux sont endémiques. Enfin, les Urticaceae groupent 11 genres et 24 espèces endémiques, indigènes ou naturalisés ; deux genres, dont un décrit par l'auteur, sont endémiques. Des espèces endémiques existent dans les genres *Elatostemma*, *Pilea* et *Pipturus*.

Les noms des auteurs de taxons sont donnés in extenso, avec les initiales des prénoms. Il est plus courant de les abréger, mais l'auteur a voulu éviter toute confusion, l'inconvénient est d'allonger singulièrement certaines citations.

En ce qui concerne les espèces, la bibliographie et les synonymes concernent essentiellement la région. Les types sont cités chaque fois que possible. Les descriptions des espèces sont précises et complètes sans pour autant être exagérément longues. Elles sont plus succinctes pour les espèces seulement cultivées. Sont également notés : les noms vernaculaires, la répartition, l'écologie, l'utilisation éventuelle. L'ouvrage est excellemment illustré par 50 planches au trait, dues pour la plupart à A. DETLOFF, certaines à J. LEMEUX, et par 2 pages de 19 photos couleurs.

On ne peut que féliciter l'auteur pour le sérieux de ce travail, ce qui laisse bien augurer de la suite qui lui sera donnée.

J. BOSSER

J.E. Vidal. *Paysages végétaux et plantes de la Péninsule indochinoise.* Agence de la Francophonie (ACCT), ed. Karthala, 248 p., 1 carte, nombreuses photos couleurs (1997).

La flore et la végétation de la Péninsule indochinoise sont aujourd'hui assez bien connues, comme l'écrit J.E. VIDAL dans l'introduction à son ouvrage. Auparavant, il signale les principales publications botaniques consacrées à cette région depuis 1790 (« Flora cochinchinensis ») jusqu'à nos jours (« Flore du Cambodge, du Laos et du Viêtnam » et « Flora of Thailand »), la plupart destinées aux spécialistes. Aujourd'hui, après de nombreuses années d'incertitude politique, les pays qui constituent cette péninsule (Thaïlande, Cambodge, Laos, Viêtnam) s'ouvrent de plus en plus au tourisme et il est heureux que les futurs visiteurs de cette région aient à leur disposition un guide en langue française qui les instruira sur les végétaux qu'on y rencontre.

La présentation de cet ouvrage est particulièrement réussie. Généreusement illustré de belles photographies en couleurs (242 au total), sa couverture est souple, la reliure solide, la rédaction soignée et la typographie variée. Dans une première partie l'auteur décrit les divers types de végétation schématisés sur une carte en couleurs et les principales formations végétales. Globalement, certaines formations sont analogues à celles qu'on observe dans d'autres régions tropicales, en particulier la végétation littorale et paralittorale (mangrove, forêts marécageuses, plages sableuses) et la végétation d'eau douce qui renferment plusieurs espèces pantropicales. Les forêts denses humides de basse altitude et de montagne sont par contre plus originales car des espèces particulières à la région (*Dipterocarpus spp.* par exemple) y dominent. Les actions destructrices de l'Homme sur la végétation (cultures sur brûlis, exploitation forestière sans contrôle, utilisation de défoliants en période de guerre) sont rappelées, ainsi que les actions protectrices (parcs nationaux, réserves naturelles, jardins botaniques). Cette première partie est illustrée de 60 photographies en couleurs de très bonne qualité qui complètent efficacement les descriptions données pour ces milieux et permettent de mieux percevoir la physionomie de ces paysages végétaux.

Dans une deuxième partie sont décrites et illustrées environ 180 espèces. Un grand nombre d'entre elles sont soit panttopicales, soit cultivées dans la plupart des régions chaudes du globe ; étant les plus communes, ce sont celles que le visiteur rencontrera le plus souvent et dont il souhaitera être informé. Cependant, on peut regretter que l'auteur n'ait pas présenté un plus grand nombre de plantes indigènes ; les 3000-4000 espèces endémiques auraient pu faire l'objet d'un chapitre particulier faisant mieux ressortir l'originalité de la flore de cette péninsule estimée à environ 15.000 espèces. Ma deuxième remarque a trait à la citation des noms d'auteurs des taxons : délibérément, et pour simplifier la présentation, lorsque les noms sont des combinaisons postérieures à la publication du basionyme, J.E. VIDAL n'a retenu comme auteurs que ceux qui ont établi ces combinaisons. Cet escamotage de l'auteur du basionyme est contraire à l'article 49 du Code international de nomenclature botanique et cette présentation serait à modifier dans les éditions futures de ce livre.

Une partie importante de l'ouvrage concerne les noms vernaculaires des espèces citées en cambodgien, laotien, thaïlandais, vietnamien, anglais et français, avec leurs équivalents scientifiques, ainsi qu'un index récapitulatif des noms scientifiques et leurs correspondants vernaculaires.

Les visiteurs des pays qui constituent cette péninsule et tous les naturalistes qui s'intéressent à cette région ont désormais à leur disposition un précieux guide de la végétation, en langue française. Écrit par l'un des meilleurs connaisseurs de la flore du sud-est asiatique après plus de 50 années de recherches sur les groupements végétaux indochinois (et tout particulièrement ceux du Laos, sujet de la thèse de doctorat que J.E. VIDAL a soutenue en 1956), cet ouvrage sera certainement très apprécié.

J. JÉRÉMIE

Instructions aux auteurs

Adansonia est une revue internationale de biologie végétale, consacrée à l'inventaire, l'analyse et l'interprétation de la biodiversité des Phanérogames. Elle publie des résultats originaux de recherches en botanique, particulièrement en systématique et domaines associés : morphologie, anatomie, biologie, écologie, phylogénie, biogéographie...

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Les manuscrits, écrits en français ou en anglais, doivent être structurés comme suit :
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- résumés écrits en français et en anglais, suivis des mots clés et « key words » ;
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CRONQUIST A. 1981. — *An Integrated System of Classification of Flowering Plants.* Columbia University Press, New York.

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